

THE EVOLUTION OF GUINEA-FOWL
(GALLIFORMES, PHASIANIDAE, NUMIDINAE)
TAXONOMY, PHYLOGENY, SPECIATION AND BIOGEOGRAPHY

By

T. M. CROWE

FitzPatrick Institute, University of Cape Town

(With 53 figures, 11 tables and 2 appendices)

[MS. accepted 15 March 1978]

ABSTRACT

Patterns of qualitative and quantitative character variation in 1 833 museum specimens encompassing all taxa attributed to the Numidinae are analysed to produce an hypothetical taxonomy and phylogeny for the subfamily. Quantitatively and ecologically defined genus, species and subspecies concepts are applied in erecting the taxonomy. A cladistic approach, based in postulated primitive-derived character sequences, is used in developing the phylogeny. 4 genera, 6 species and 16 subspecies are recognized. Cladistic events are linked to likely causal geological and palaeoecological events to determine a possible evolutionary chronology. Genera are thought to have arisen as a consequence of Miocene and Pliocene radiations; species and subspecies as a result of Pleistocene divergence. An hypothetical map of African avifaunal zones, based on evolutionary patterns found in guinea-fowl, is offered. Comparisons of this map with other African avifaunal maps and with distribution maps of selected francolin taxa suggest that biogeographic patterns found in guinea-fowl reflect broad patterns found in many African birds. An hypothesis as to the causes of relatively high species richness in francolins is offered.

CONTENTS

	PAGE
Introduction	44
Methods	45
Material and characters	45
Taxonomic philosophy	45
Taxonomic methodology	50
Phylogenetic philosophy	51
Phylogenetic methodology	52
Speciation	52
Biogeography	52
Results, discussion and conclusions	56
Taxonomy	56
Genera	56
Species and subspecies	56
Taxonomic summary	98
Phylogeny	118
Primitive and derived character states	118
Phyletic analysis	120
Speciation	121
Origin and derivation of the Numidinae	121
Evolution of genera	122
Evolution of species and subspecies	122
Biogeography	123
Results	123
Discussion	123
Conclusions	125

	PAGE
Synthesis	126
Acknowledgements	130
References	130
Appendix 1	133
Appendix 2	134

INTRODUCTION

There are many reasons why an understanding of the evolution of guinea-fowl (Numidinae; Sibley & Ahlquist 1972) should provide an insight into patterns of avian evolution and biogeography in Africa.

1. The Numidinae are endemic to Africa, and presumably evolved and/or radiated there from a francolin-like ancestor (Ghigi 1936; Cracraft 1973; Olson 1974).

2. At least one guinea-fowl species has become adapted to life in each major terrestrial African biome outside of desert, Mediterranean vegetation and montane forest (Crowe & Snow 1978).

3. Guinea-fowl are sedentary birds (Chapin 1932*a*; Priest 1933; Archer & Godman 1937; Elgood *et al.* 1973), and thus should be more susceptible to local selection pressures than would be more mobile species (Ehrlich & Raven 1969).

4. The distributions of some guinea-fowl taxa do not correlate well with present-day vegetation and topography (Chapin 1932*a*). Such anomalous distributions of plants and animals can be used to infer environmental conditions and the distributions of African biomes during the Tertiary and Quaternary (Chapin 1932*a*; Moreau 1963, 1966; Roberts 1975; Hamilton 1974; Axelrod & Raven 1978).

5. The genetic basis of morphological variation in several guinea-fowl species is relatively well understood (Ghigi 1936).

6. Perhaps most importantly, guinea-fowl species are relatively well represented in museum collections and, accordingly, lend themselves to quantitative analysis, which is desirable in formulating precise evolutionary and biogeographic hypotheses (Mayr *et al.* 1953; F. Vuilleumier 1975).

Thus, guinea-fowl provide a simple, characteristically African system from which evolutionary and biogeographic hypotheses may be derived. The aims of the present study are to:

1. re-examine and revise, if necessary, the rather confused taxonomy within the subfamily (Table 1), using a repeatable, relatively objective quantitative methodology;
2. produce a parsimonious phylogeny based on the analysis of shared derived character states;
3. develop models of speciation, which are consistent with the phylogeny developed herein and the likely past geological and climatic history of Africa;

4. suggest tentative avifaunal subregions, provinces and districts for Africa, based on analysis of the distributions of recognized guinea-fowl taxa.

The possible familial status of the subfamily (Wetmore 1960), the adaptiveness of inter- and intra-specific morphological variation in guinea-fowl, and the predictive value of evolutionary and biogeographic models based on patterns found in guinea-fowl, will be discussed briefly, if at all, herein. These topics will be dealt with in greater detail in future papers.

METHODS

MATERIAL AND CHARACTERS

The author examined 1 833 museum specimens, including all taxa attributed to the subfamily in Table 1. All characters investigated (Appendices 1 and 2, Figs 2–4) appear to have a genetic basis (Ghigi 1936), and have been discussed in previous studies (e.g. Beddard 1898; Bannerman 1930; Chapin 1932a; Ghigi 1936; Archer & Godman 1937; Jackson 1938; Boetticher 1954; Mackworth-Praed & Grant 1952, 1962, 1970). Therefore, they need not be described again in detail. Characters were chosen to reflect as much of the phenotype as possible, while eliminating the necessity of close comparisons of specimens from different collections. Due to logistical constraints (e.g. small sample sizes of each sex, time allotted for examination of specimens, and variation in the detail of collectors' notes and care in specimen preparation) some of the quantitative characters listed in Appendix 1 were assessed relatively subjectively, and data for both sexes were lumped. This introduces a certain amount of imprecision into the analysis. But, subjective assessments were made against a set of reference specimens, photographs or drawings encompassing the range of observed variation. Also, the previous studies mentioned above have stated that sexual dimorphism is absent, or relatively minor in comparison with geographical variation in guinea-fowl. Moreover, it was felt that the advantages accruing from considering a large number of characters for many specimens outweighed any sampling bias due to imprecise measurement and sexual dimorphism.

TAXONOMIC PHILOSOPHY

The taxonomic philosophy adhered to in the present study follows that outlined by Mayr *et al.* (1953). A species is a group of actually or potentially interbreeding individuals which has diverged sufficiently in allopatry to have become reproductively isolated from other such groups. A genus is a monophyletic taxon which is decidedly qualitatively distinct, and is adapted to a particular mode of life, i.e. a generic 'niche'.

The subspecies is much more difficult to define. Table 1 shows that much of the 'taxonomic variation' in guinea-fowl systematics is at the subspecies level. Some systematists (e.g. Wilson & Brown 1953; Moreau 1957; Selander 1971; Gould & Johnston 1972) state that the category is useless, and even

TABLE 1
A history of the taxonomy of guinea-fowl.¹

Taxa	Chapin (1932 <i>a</i> and <i>in litt.</i>)	Peters (1934)	Ghigi (1936)	Boetticher (1954)	Mackworth- Praed & Grant (1952; 1962; 1970)	White (1965)	Crowe (this study)
<i>Phasidus</i>	×	×	×	×	×		
<i>Agelastes</i>						×	×
<i>niger</i>						×	×
<i>niger</i>						×	×
<i>meleagrides</i>						×	×
<i>vulturinum</i>						×	×
<i>plumifera</i>						×	×
<i>plumifera</i>						×	×
<i>schubotzi</i>						×	×
<i>edouardi</i>						×	×
<i>edouardi</i> ⁴						×	×
<i>suahelica</i>							
<i>schoutedeni</i>						×	×
<i>seth-smithi</i>						×	×
<i>verreauxi</i> ²						×	×
<i>sclateri</i>						×	×
<i>chapini</i>						×	×
<i>granti</i>						×	×
<i>barbata</i>						×	×
<i>lividicollis</i>						×	×
<i>kathleenae</i> ³						×	×
<i>symonsi</i>						×	×
<i>pucherani</i>						×	×
<i>meleagris</i>						×	×
<i>Numida</i>							
<i>meleagris</i>							
<i>meleagris</i>							

TABLE I
A history of the taxonomy of guinea-fowl.¹

Taxa		Chapin (1932a and in litt.)	Peters (1934)	Ghigi (1936)	Boetticher (1954)	Mackworth- Praed & Grant (1952; 1962; 1970)	White (1965)	Crowe (this study)
<i>Phasidus</i>	<i>niger</i>	x	x	x	x	x		x
<i>Agelastes</i>	<i>niger</i>						x	x
	<i>meleagrides</i>	x	x	x	x	x	x	x
<i>Acryllium</i>	<i>vulturinum</i>	x	x	x	x	x	x	x
<i>Guttera</i>	<i>plumifera</i>	x	x	x	x	x	x	x
	<i>plumifera</i>	x	x	x	x	x	x	x
	<i>pucherani</i> ⁴	x	x			x		
	<i>edouardi</i> ⁴	x	x	x	x	x	x	x
	<i>suahelica</i>			x	x			
	<i>schoutedeni</i>	x	x	x	x	x	x	
	<i>seth-smithi</i>	x	x	x	x	x	x	x
	<i>verreauxi</i> ²	x	x	x	x	x	x	x
	<i>sclateri</i>	x	x		x	x	x	
	<i>chapini</i>	x	x		x	x	x	
	<i>granti</i>	x		x			x	
	<i>barbata</i>		x	x		x	x	x
	<i>lividicollis</i>			x	x			
	<i>kathleenae</i> ³	x				x	x	
	<i>symonsi</i>					x		x
	<i>pucherani</i>			x	x			x
<i>Numida</i>	<i>meleagris</i>	x	x	x	x	x	x	x
	<i>meleagris</i>	x	x	x	x	x	x	x
	<i>major</i>	x	x	x	x	x	x	x
	<i>somaliensis</i>	x	x	x	x	x	x	x
	<i>intermedia</i>	x	x	x	x	x	x	x
	<i>toruensis</i>	x	x	x	x	x	x	x
	<i>neumanni</i>			x				
	<i>omoensis</i>			x				
	<i>ansorgei</i>			x				
	<i>inermis</i>							
	<i>sabyi</i>	x	x	x	x			x
	<i>galeata</i>	x	x	x	x	x	x	x
	<i>marchei</i>	x	x	x	x	x		
	<i>strasseni</i>	x	x	x	x	x	x	
	<i>mitrata</i>	x	x	x	x	x	x	x
	<i>reichenowi</i>	x	x	x	x	x		x
	<i>marungensis</i>	x	x	x	x	x	x	x
	<i>callewaerti</i>	x	x	x	x	x	x	
	<i>maxima</i>	x	x	x	x			
	<i>uiehensis</i>			x	x			
	<i>rikwae</i>			x	x			
	<i>frommi</i>			x				
	<i>coronata</i>	x	x	x	x		x	x
	<i>limpopoensis</i>		x		x			
	<i>transvaalensis</i>				x			
	<i>papillosa</i>	x	x	x	x	x	x	
	<i>damarensis</i>	x	x	x	x	x	x	x
	<i>blancoui</i> ³				x			
	<i>reichenowi</i>						x	

¹ Unless otherwise specified, nomenclature follows Peters (1934).

² *G. e. verreauxi* = *G. e. pallasi*, see White (1965).

³ See White (1965).

⁴ Since these two taxa are considered to be conspecific in the present study, following the principle of priority the specific name recognized is *G. pucherani*.

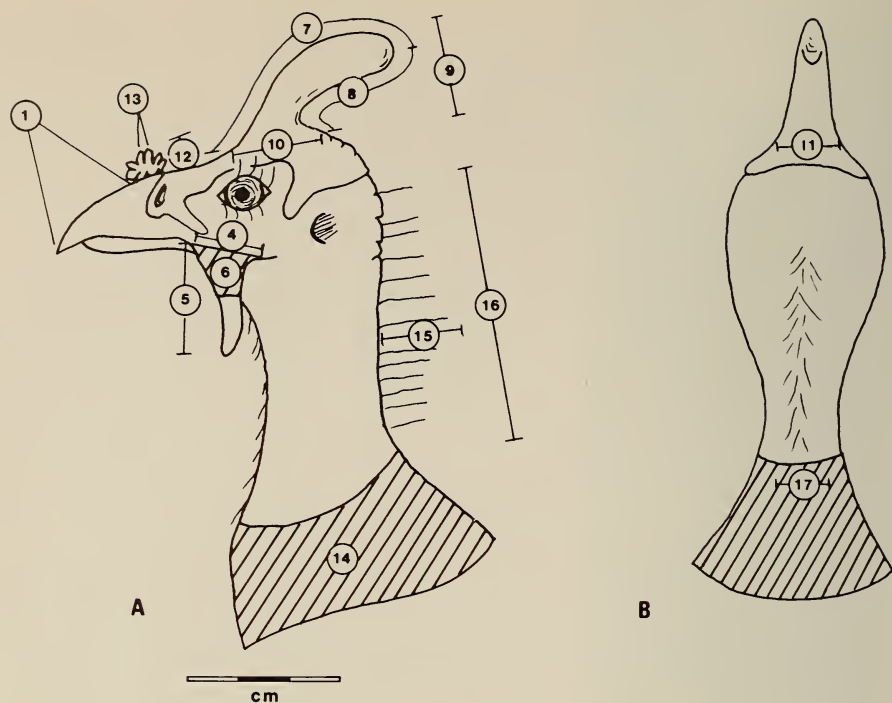


Fig. 2. Quantitative characters 1, 4-17. A. Lateral view of head, neck and collar of *Numida meleagris*. B. Dorsal view of the same.

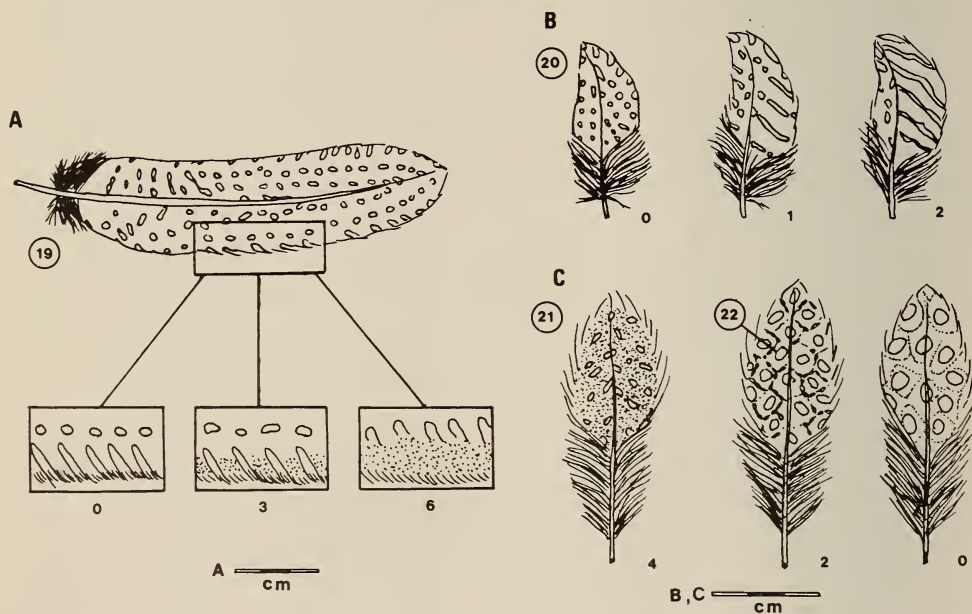


Fig. 3. Quantitative characters 19-22. A. Secondary remex from *Numida meleagris*. B. Wing covert from *N. meleagris*. C. Mid-dorsal feather of the same.

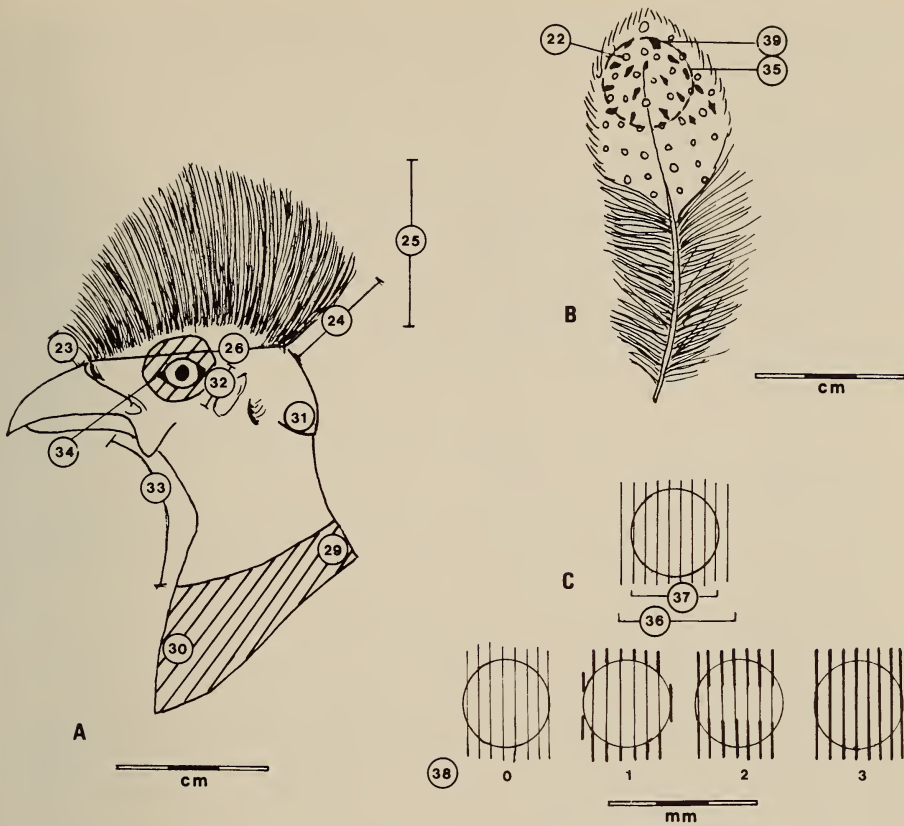


Fig. 4. Quantitative characters 22-26, 29-39. A. Lateral view of head, neck and collar of *Guttera plumifera*. B. Mid-dorsal feather of *G. pucherani edouardi*. C. Spots on mid-dorsal feathers of *Guttera* spp.

detrimental to the understanding of geographic variation and intra-specific evolution. These critics maintain that:

1. characters used to delineate subspecies usually have patterns of geographic variation which are discordant with each other and with the distribution attributed to the taxon;
2. indistinguishable phenotypes occur in geographically isolated areas, presumably due to parallel evolution under similar selective regimes;
3. no objective degree of difference can be offered to distinguish subspecies from slightly differentiated local populations.

In an attempt to satisfy these legitimate criticisms, Ford (1974) offers the taxo-evolutionary subspecies concept, the concept adhered to in the present study. This concept limits the awarding of subspecies status to geographic aggregates of populations which appear to have undergone genetic and phenotypic divergence in allopatry. Past allopatric divergence may be inferred for

presently parapatric taxa if their distributions can be derived from concordant character variation, and if they are separated by a zone of secondary intergradation (Ford 1974).

TAXONOMIC METHODOLOGY

Since both the recognition of taxa and their assignment to taxonomic categories (with the possible exception of the species) are ultimately subjective processes (Mayr *et al.* 1953; Selander 1971; Ford 1974), it is of utmost importance to outline the methodology underlying taxonomic decisions.

With the foregoing taxonomic philosophy in mind, the procedure used to determine genera involved four steps:

1. a sorting of specimens into groups which consisted of members of both sexes, and which possessed unique combinations of qualitative characters;
2. a cluster analysis of these groups according to the number of shared qualitative character states;
3. presentation of the clustering similarity matrix in the form of a phenogram;
4. interpretation of the matrix and the phenogram, according to the taxonomic philosophy outlined above, to determine genera.

Once genera were identified, each was analysed separately to determine species and subspecies. Two multivariate statistical computer programmes were used in tandem in these analyses. The first programme, BMDP2M (Dixon 1975), was used to cluster specimens into operational taxonomic units (OTUs, Sneath & Sokal 1973). In BMDP2M, the clustering algorithm first amalgamates the two specimens which are most similar. The amalgamated specimens are then treated as one case in future comparisons. This clustering algorithm continues until all specimens are grouped into one large cluster. The similarity measure used is the Euclidean distance, and the clustering method is the weighted average pair group method (Sneath & Sokal 1973). The printed output of BMDP2M includes a phenogram which illustrates the results of the cluster analysis in a hierarchical manner. OTUs were identified from examination of these phenograms. In a phenogram, OTU status was awarded to any specimen cluster which contained members of both sexes from several geographically contiguous localities, and which was morphologically more distinct (i.e. linked up with other such groups at a lower similarity) than was a group of specimens from a single, relatively well-sampled locality within the range of an undisputed taxon listed in Table 1.

OTUs were compared using stepwise multiple discriminant analysis programme BMDP7M (Dixon 1975). This programme calculates a series of linear classification functions in a stepwise manner, such that within-OTU variance is minimized and between-OTU variance maximized. At each step in the analysis, the character not yet entered into the functions that best separates OTUs is included. This procedure continues until all significant ($P < 0.05$) characters are included in the functions. The printed output of BMDP7M

includes a probabilistic statement as to the OTU membership of each specimen. In the final step, BMDP7M computes canonical discriminant functions between OTUs, and plots the first two so as to give an optimal two-dimensional picture of the separation of the OTUs. This plot consists of a multivariate centroid for each OTU, surrounded by a cloud of individual points corresponding to specimens in that OTU. In this study, an OTU, or group of OTUs, was awarded species rank if none of the component specimens were intermediate between two OTUs (i.e. were assigned a probability greater than 0.05 of belonging to another OTU).

Once species were identified, character variation within each species consisting of several OTUs was analysed to determine if any component OTUs merited subspecies status. The taxonomic procedure used in these analyses involved four steps:

1. division of the species range into uniform areas;
2. computation of mean values and coefficients of variation (COV, Sokal & Rohlf 1969) for each character for each area;
3. contour mapping of mean values for each character, and of the total COV for all characters for each area;
4. interpretation of the contour maps to determine OTUs whose distributions could be derived from concordant character variation, and whose boundaries were circumscribed by a zone of secondary intergradation.

Subspecies rank was awarded to any OTUs whose distributions could be derived from concordant variation in at least three characters, and which enclosed an area of relatively low total COV bounded by an area(s) of high total COV. Areas with relatively low variability (i.e. low total COV) were taken to be probable 'core regions' for their associated subspecies. Areas with relatively high variability (i.e. high total COV) were taken to be regions of secondary intergradation.

The smallest uniform area that produced sample sizes that were statistically adequate was that enclosed by a block four degrees on a side. Contour mapping was done with the assistance of a computer, using contouring programme GPCP (CALCOMP 1971). This programme fits an approximate contour surface to the data using least squares polynomial analysis.

PHYLOGENETIC PHILOSOPHY

A cladistic approach (Marx & Rabb 1970; Cracraft 1972) was used to infer phylogenetic relationships between guinea-fowl genera and species. Cladistic analysis involves discernment and use of derived character states. Derived states are those which are unique or relatively restricted to the taxa under study, or which could be adaptive in a social or ecological context (Marx & Rabb 1970). Shared primitive character states, i.e. those commonly inherited from distant ancestors, cannot be used to unite more recently evolved taxa (Cracraft 1972). Other than its consistent, relatively objective methodology, the major advantage of a cladistic analysis is that a proposed phylogeny can be

refuted on clearly specified grounds. A proposed phylogeny must be modified or abandoned if: derived characters used to produce it are shown to be primitive; another interpretation of the same or different combination of derived character states yields a more parsimonious phylogeny, i.e. requiring fewer convergences; a fossil form is found which possesses a character suite incompatible with the proposed phylogeny; or if it is grossly at variance with known biogeographic events (Cracraft 1972; F. Vuilleumier 1975).

PHYLOGENETIC METHODOLOGY

Since the presumed ancestor of the guinea-fowl is a francolin-like phasianid (Ghigi 1936), any character state common among extant francolins or guineafowl-phasianid hybrids was taken to be primitive. Ghigi (1936), Mackworth-Praed & Grant (1952, 1962, 1970) and Hall (1963) were used as sources of information on francolins. Ghigi (1936), Bourke (1967) and R. Chapin (*in litt.*) were the sources of information on the phenotypes of hybrids. Any character state unique to, or relatively common among, guinea-fowl species was taken to be derived.

Once hypothetical primitive-derived sequences of character states were determined, a parsimonious phylogeny was produced following methods outlined by Cracraft (1972).

SPECIATION

There is now widespread agreement among evolutionary biologists and biogeographers that speciation, extinction and drastic distributional shifts in plants and animals have been common and world-wide during the Tertiary and Quaternary (Moreau 1966; B. Vuilleumier 1971; Axelrod & Raven 1978). As mentioned in the introduction, past geological and climatic events have almost certainly helped to shape patterns of speciation and biogeography in Africa. Several authors (Chapin 1932a; Cooke 1962; Howell & Bourlière 1963; Moreau 1966; Carcasson 1964; Butzer 1967; Hamilton 1974; Axelrod & Raven 1978) have given maps of Africa depicting the hypothetical distribution of vegetation during relatively wetter and/or drier conditions in the past. Livingstone (1975), Hamilton (1974) and Axelrod & Raven (1978) have provided some temporal estimates for climatic and geological events which may have caused these conditions. As a preface to this study, the various hypothetical vegetation maps were compared, and compromise 'wet' and 'dry' maps (Figs 5-6) were drawn which incorporated salient features of each. An hypothetical pattern and chronology for speciation in guinea-fowl were developed by relating the phylogeny derived herein to present-day (Fig. 7) and hypothetical past 'wet' and 'dry' vegetation maps in the light of temporal estimates given by authors mentioned above.

BIOGEOGRAPHY

Once the taxonomy and phylogeny of a group are defined, biogeographic hypotheses based on patterns found in that group may be formulated. Since

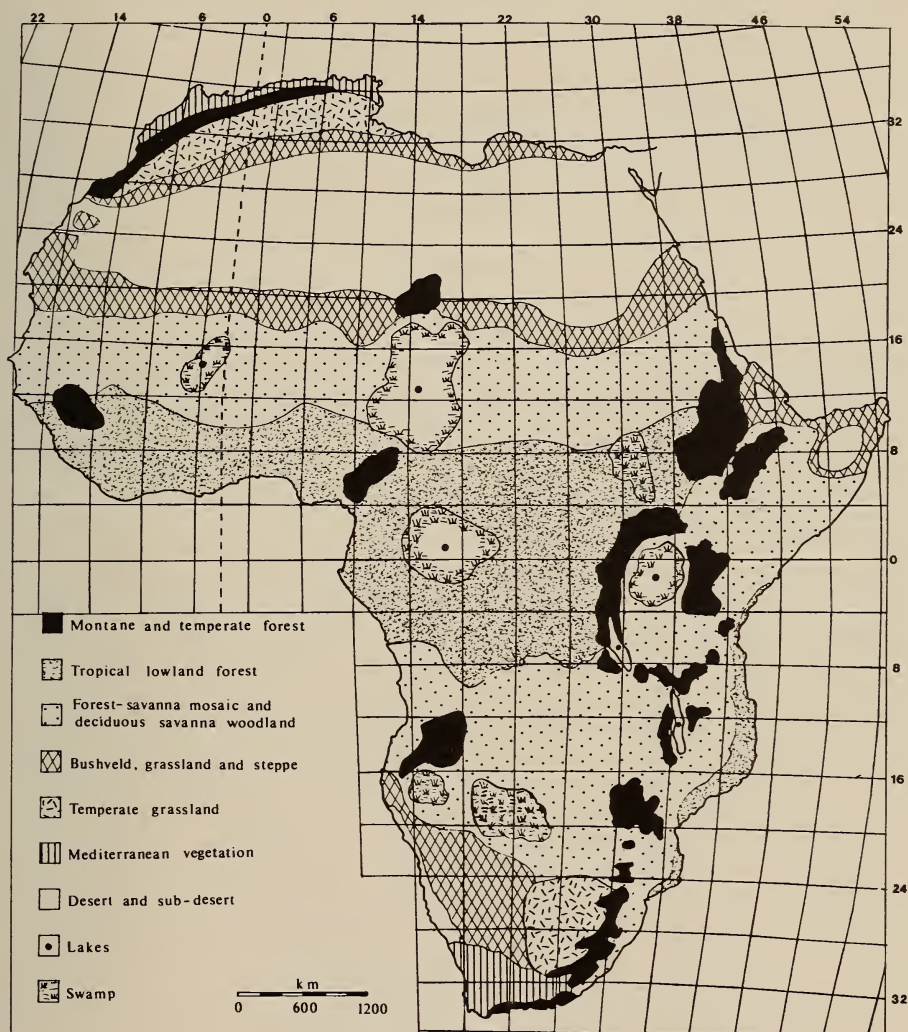


Fig. 5. Hypothetical vegetation map of Africa during a wetter period.

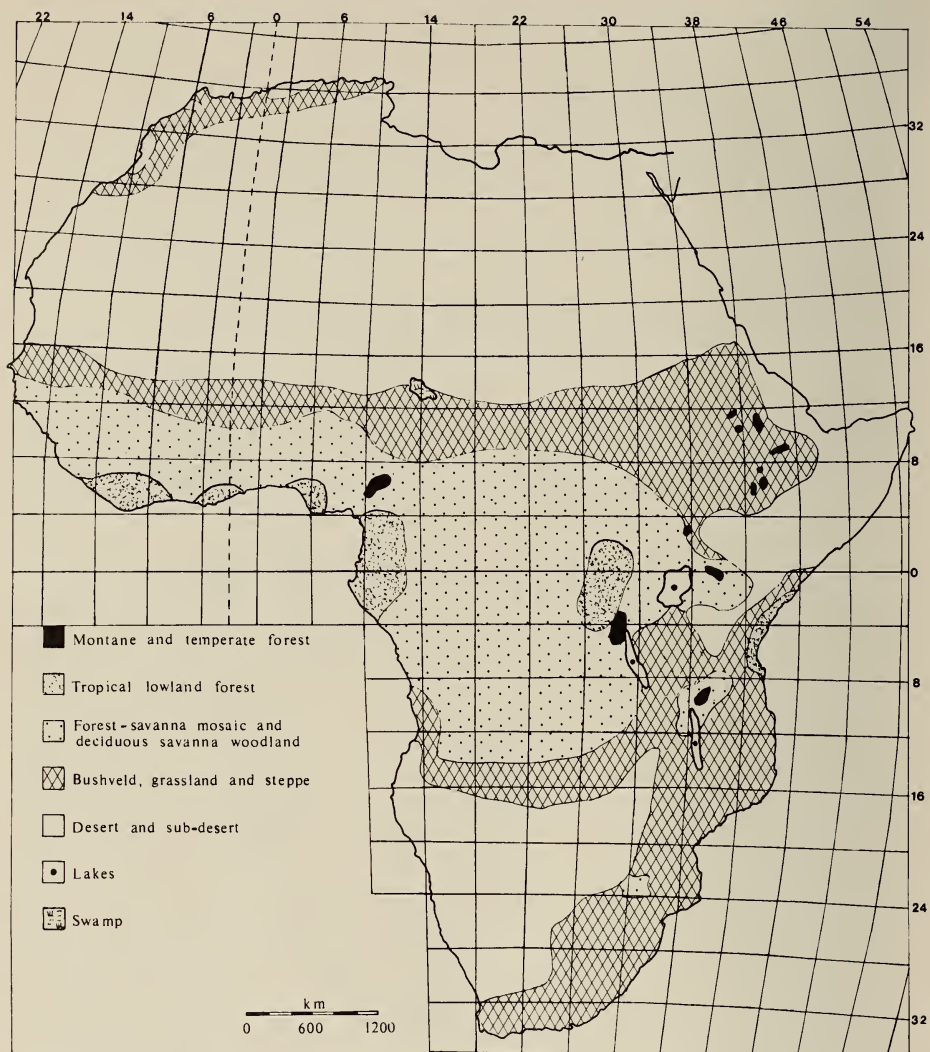


Fig. 6. Hypothetical vegetation map of Africa during a drier period.

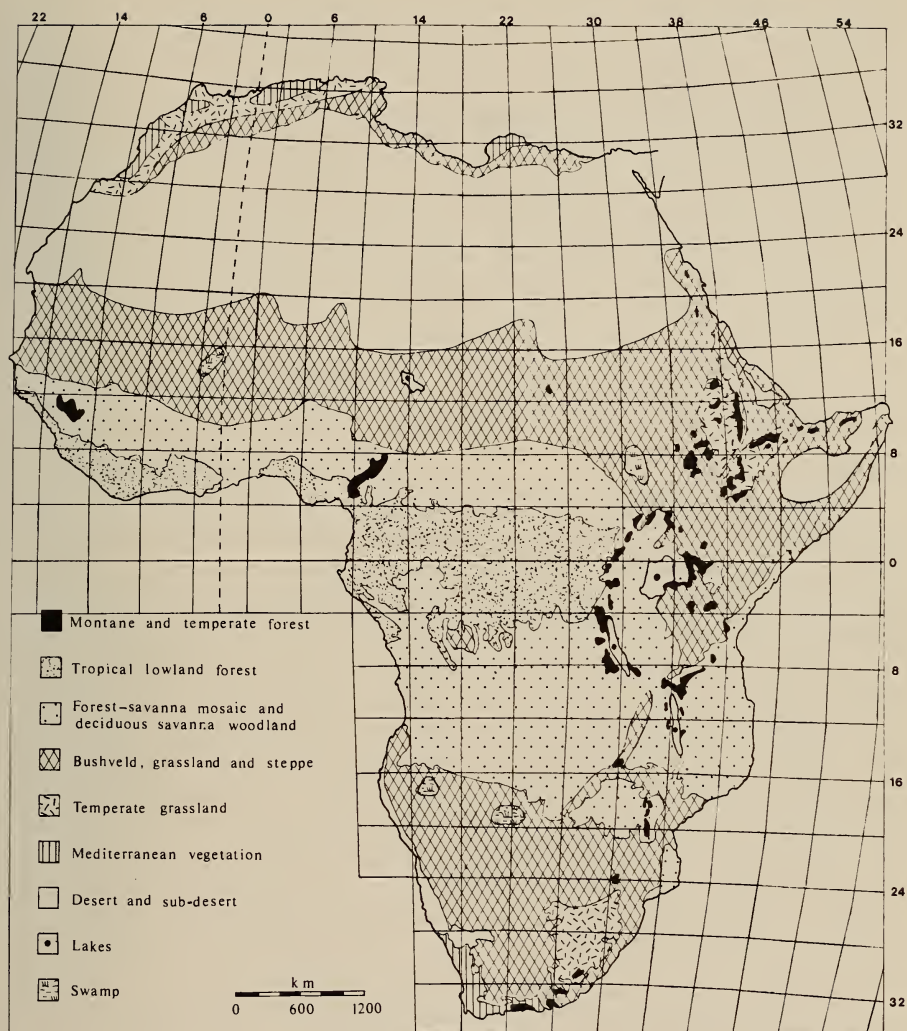


Fig. 7. Present-day vegetation map of Africa.

guinea-fowl are sedentary, stenotopic animals, the distribution of a given taxon should reflect the geographical limits and temporal stability of its associated biome. If a taxon has a vicariated distribution, it is likely that the vicars (see Udvardy 1969) were isolated as a result of past partitioning of its biome. However, if a taxon shows little geographic variation, its biome probably has not been fragmented in the past. In this study, the boundaries of recognized genera, species and subspecies were used to formulate an hypothetical avifaunal map of Africa. Boundaries of taxonomically homogeneous genera (i.e. with no subspecies) were used to delimit African avian subregions in this map. In other words, a subregion is any biome which has presented its associated guinea-fowl taxa with a sufficiently consistent selective regime to produce a monotypic genus, or a genus composed of monotypic species. Species boundaries were used to delimit provinces, and subspecies boundaries to delimit districts, following a similar reasoning used in defining subregions.

RESULTS, DISCUSSION AND CONCLUSIONS

TAXONOMY

GENERA

There are fourteen groups of guinea-fowl specimens (Table 2) which possess unique combinations of the qualitative characters listed in Appendix 1. These groups are termed operational genera (OG). In the light of habitat preference information summarized by Crowe & Snow (1978), the results of a cluster analysis of the OG (Fig. 8) suggest that there are four genera in the Numidinae. These are labelled A–D in Figure 7, and become apparent at the similarity level of eleven shared characters. In Table 1, genus A corresponds to the genera *Agelastes* Bonaparte, 1850, and *Phasidus* Cassin, 1857; genus B to *Guttera*; genus C to *Acryllium*; and genus D to *Numida*. Genus A must be named *Agelastes*. The following section consists of a taxonomic summary including taxonomic conclusions, brief descriptions and mensural statistics, and a discussion of taxonomic conclusions when deemed necessary. All recognized genera are said to be largely restricted to broad 'niches' (Crowe & Snow 1978). The genus *Agelastes* is found only in dense tropical lowland forest. The genus *Guttera* is also limited to forest areas, but inhabits riverine forest and the forest edge as well as tropical lowland forest. The genus *Acryllium* is confined to the subdesert steppe of north-eastern Africa. The genus *Numida* can be found in virtually all areas of non-forested Africa outside of desert, Mediterranean and montane vegetation.

SPECIES AND SUBSPECIES

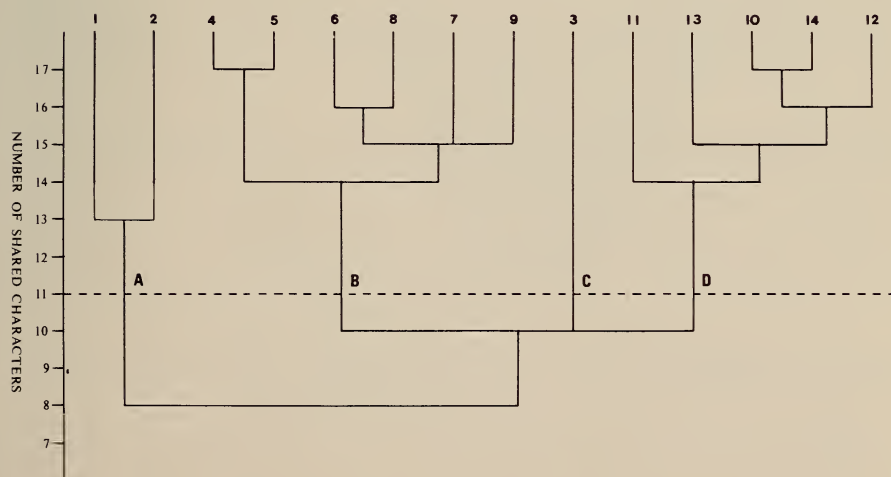
The genus *Acryllium* appears to be monotypic. A cluster analysis of 43 *Acryllium* specimens (Fig. 9) according to 7 quantitative characters (nos 1–5, 41–42 in Appendix 2) yields only one OTU. Six individuals from Mt Kunchurro, Boran, Ethiopia (c. 4°30'N 38°E), link to form a cluster at a level (indicated

TABLE 2

Operational genera derived from analysis of qualitative character states listed in Appendix 1.

Character	Operational genera													
no.	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1	1	3	3	2	2	2	2	2	2	4	4	4	4	4
2	5	5	1	3	3	3	3	3	4	2	5	2	5	2
3	1	4	4	4	3	4	4	4	4	2	1	2	2	2
4	1	1	2	2	2	2	1	2	2	2	2	2	2	2
5	1	1	2	2	2	1	1	2	2	2	2	2	2	2
6	1	1	1	1	1	2	2	2	1	1	1	1	1	1
7	1	1	1	2	2	1	1	1	1	3	3	2	2	3
8	1	1	2	2	2	2	2	2	2	1	2	3	3	1
9	1	1	1	1	1	1	1	1	1	1	2	1	2	1
10	1	7	6	5	5	2	5	2	4	3	3	5	3	3
11	1	1	2	3	3	3	3	3	4	2	2	2	2	2
12	1	1	2	2	2	2	2	2	2	2	2	2	2	2
13	1	1	1	2	2	2	2	2	2	2	2	2	2	2
14	1	1	2	1	1	1	2	2	2	1	1	1	1	1
15	1	1	3	2	2	2	2	2	4	4	4	4	4	4
16	1	1	1	2	2	2	2	2	2	1	1	1	1	1
17	?	?	2	1	1	1	1	1	1	1	1	1	1	1
18	1	1*	2	4	4	4	4	4	4	3	3	3	3	3

* Only in the juvenile bird.

Fig. 8. The results of a cluster analysis of OG in Table 2. A. *Agelastes*. B. *Guttera*. C. *Acryllium*. D. *Numida*.

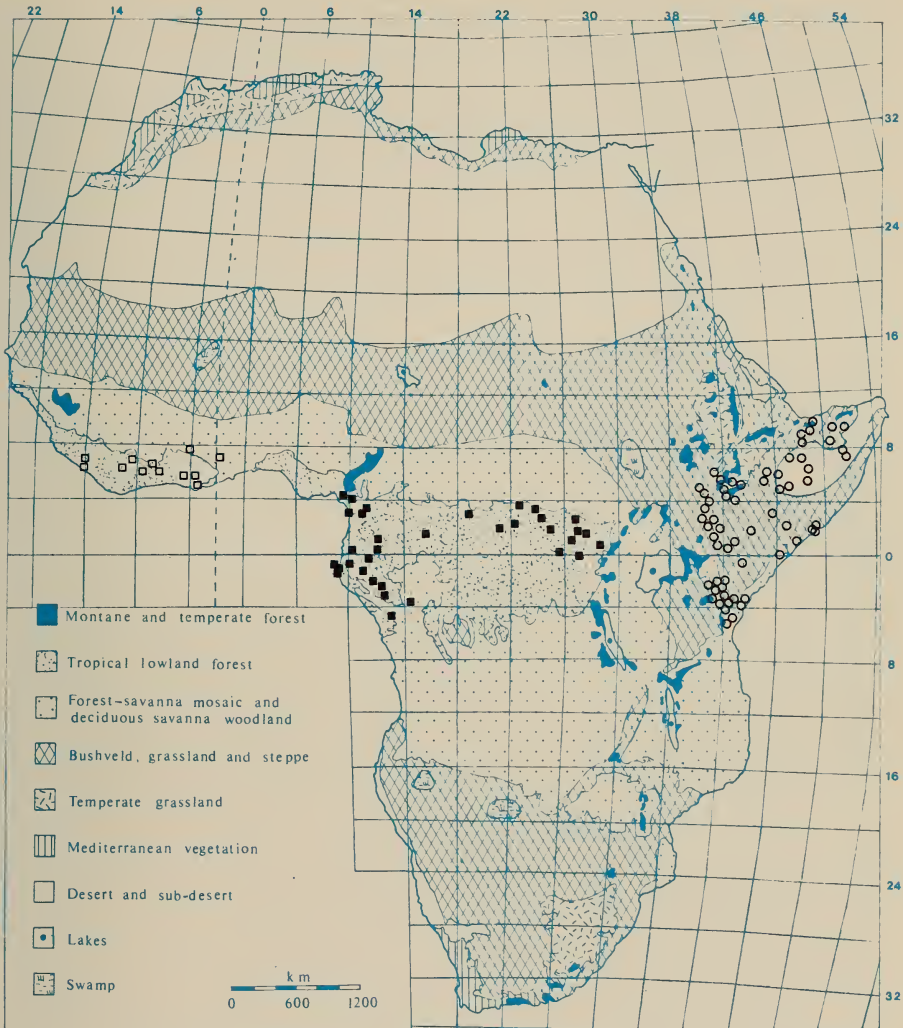


Fig. 10. The distributions of *Agelastes meleagrides* (□), *Agelastes niger* (■), and *Acryllium vulturinum* (○).

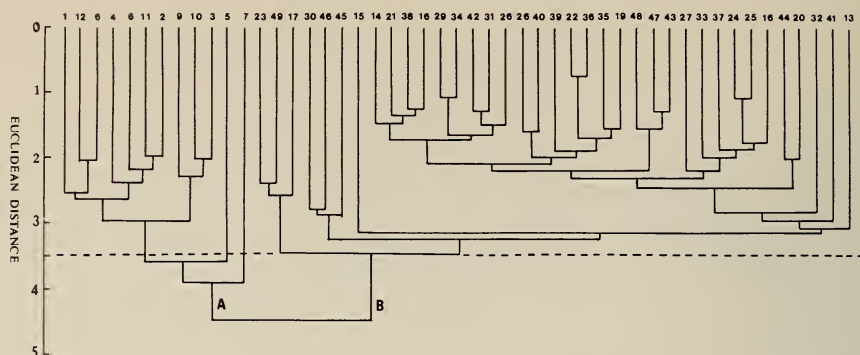


Fig. 11. The results of a cluster analysis of forty-nine specimens of *Agelastes*. A. *A. meleagrides*. B. *A. niger*.

Agelastes meleagrides and OTU B to *A. niger*. The distributions of these species are plotted in Figure 10.

The remaining two genera are taxonomically more complex than are the first two. The results of a cluster analysis of 494 *Guttera* specimens according to 24 quantitative characters (nos 1–5, 22–40 in Appendix 2) are summarized in Figure 12A. The dashed line in Figure 12A indicates the level at which twelve individuals from Ngayu, Zaïre ($1^{\circ}45'N$ $27^{\circ}15'E$), link to form a cluster. Seven OTUs are recognized. A discriminant functions analysis (Fig. 13) suggests that there are two groups of OTUs between which there are no intermediate individuals. These OTU groups are recognized as species. The first species, comprising OTUs 1 and 2, corresponds to *G. plumifera* in Table 1. The second species, comprising OTUs 3–7, corresponds to two commonly recognized species, *G. pucherani* (Hartlaub), 1860, and *G. edouardi* (Hartlaub), 1867 (Table 1). Following the law of priority, this species must be named *G. pucherani*.

The two OTUs comprising *Guttera plumifera* partition the distribution of that species into eastern and western portions. The distributions of these OTUs (Fig. 14) are delineated by patterns of variation in fifteen of the sixteen quantitative characters which vary in *G. plumifera*. Contour maps of variation in these characters, and of the total COV for six areas (Fig. 15) within the distribution of *G. plumifera* are given in Figures 16 and 17. Two types of character variation, 'mountain-valley' and clinal variation, are apparent in these contour maps. 'Mountain-valley' variation occurs when eastern and western OTUs have similar values, and are separated by a transition area(s) with higher ('mountains') or lower ('valleys') values. Characters which show 'mountain-valley' variation are: bill length (Fig. 16B), wing length (Fig. 16C), tarso-metatarsus length (Fig. 16D), wattle length (Fig. 16F), crest frontal length (Fig. 16G), crest basal length (Fig. 17J), dorsal spot number (Fig. 17K), total spot barbs (Fig. 17M), and total within-spot barbs (Fig. 17N). Characters which show clinal variation are: occipital fold (Fig. 16A), wattle basal width (Fig. 16E), crest rear length (Fig. 16H), dorsal spot size (Fig. 17L), ear patch

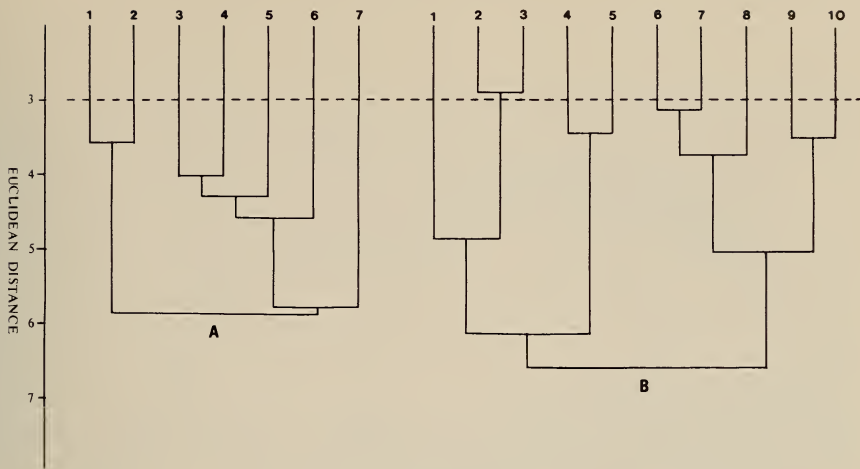


Fig. 12. The results of a cluster analysis. A. *Guttera* specimens B. *Numida* specimens.

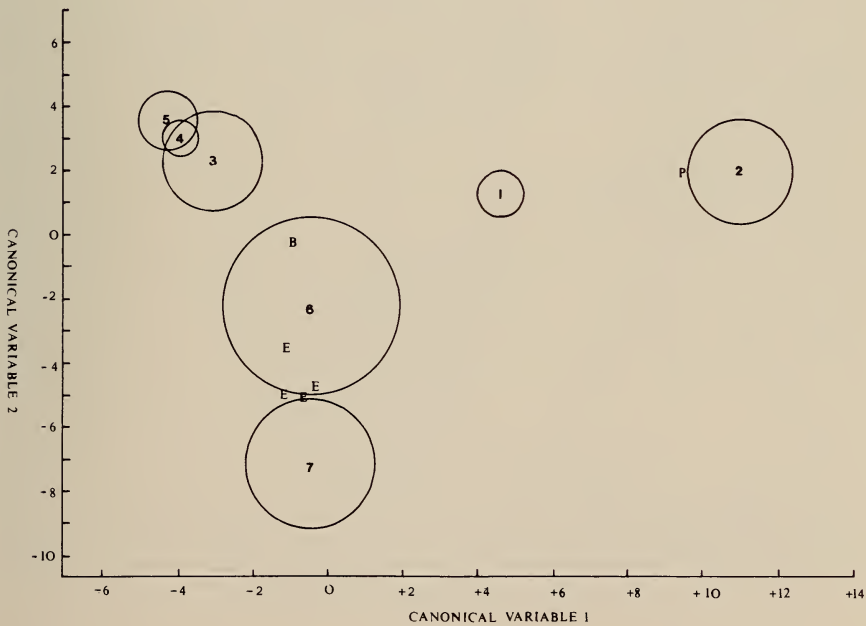


Fig. 13. A discriminant functions analysis of *Guttera* OTUs. Circles encompass 90 per cent of the individuals assigned to each OTU. Only intermediate specimens between non-overlapping OTUs are plotted. B — intermediate between OTUs 5 and 6; E — intermediate between OTUs 6 and 7; P — intermediate between OTUs 1 and 2.

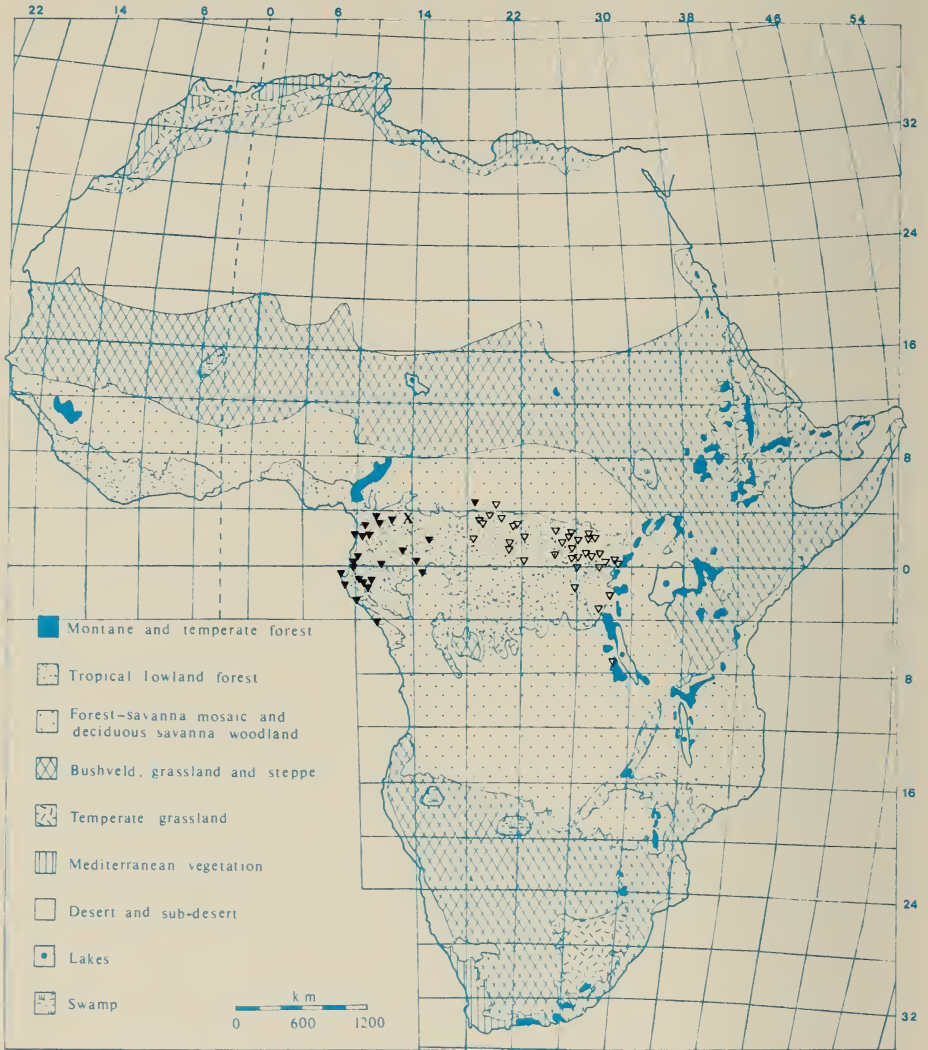


Fig. 14. The distribution of *Guttera plumifera plumifera* (▼) (= OTU 2), *G. p. schubotzi* (▽) (= OTU 1), and a single intergrade (X).



Fig. 15. Areas used in contour map analysis of *Guttera* spp. Those areas marked with an 'X' have data for both species. Those marked with a 'P' have data for *G. plumifera* only, and those without notation for *G. pucherani* only.

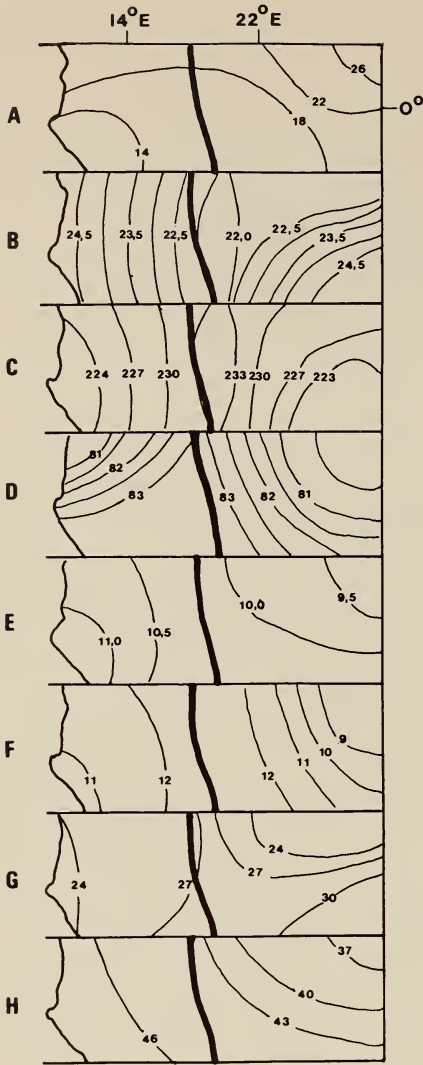


Fig. 16. Contour maps of character variation in *Guttera plumifera*. A. Occipital fold. B. Bill length. C. Wing length. D. Tarso-metatarsus length. E. Wattle width. F. Wattle length. G. Crest frontal length. H. Crest rear length. OTU boundaries are indicated by thick lines.

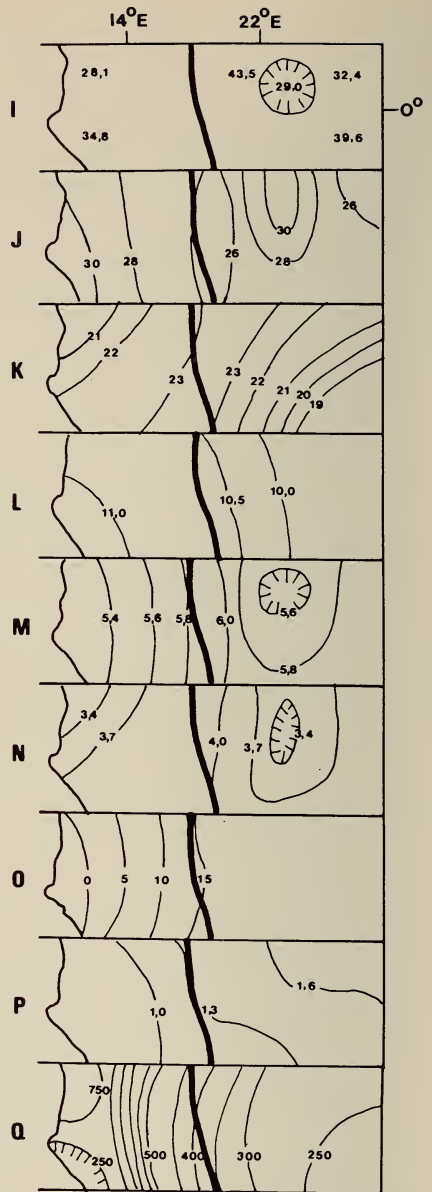


Fig. 17. Contour maps of character variation and total COV for *Guttera plumifera*. I. Crest central height. J. Crest basal length. K. Dorsal spot number. L. Dorsal spot size. M. Total spot barbs. N. Total within spot barbs. O. Ear patch. P. Spot barb blueness. Q. Total COV. OTU boundaries are indicated by thick lines.

(Fig. 17O), and spot barb blueness (Fig. 17P). These well-defined OTUs each have a region of relatively low total COV (*c.* 250) within their distributions, and are separated by a transition area with a relatively high total COV (*c.* 750) (Fig. 17Q). Thus, both OTUs meet the criteria set for subspecies (see *Taxonomic methodology*). In Table 1, the western subspecies (OTU 2) corresponds to *G. p. plumifera*, and the eastern subspecies (OTU 1) to *G. p. schubotzi*. In statistical comparisons, these subspecies differ significantly ($P \leq 0.05$; *t* test) in eight characters. *Guttera plumifera plumifera* has significantly higher values for bill length, wattle basal width, wattle length, crest rear length, and crest basal length. *Guttera plumifera schubotzi* has higher values for occipital fold, ear patch, and spot barb blueness. Means and standard deviations for these and other characters are given in the section below.

Approximate geographic distributions of the five OTUs comprising *G. pucherani* are shown in Figure 18A. Contour maps of twenty-three characters which vary in this species (nos 1–5, 22–31, 33–40 in Appendix 2) are given in Figures 19–30A. In these maps, the distributions of all five OTUs are delineated from those of their neighbours by statistically significant patterns of variation in six to seventeen of the characters analysed. The results of all possible pairwise statistical comparisons (*t* tests) between neighbouring OTUs are summarized in Tables 4 and 5. A contour map of variation in total COV for twenty-five areas (Fig. 15) within the distribution of *G. pucherani* is given in Figure 30B. This figure shows that the distributions of all five OTUs enclose or fall within a region of relatively low total COV (200–400). For all OTU distributions but one, that of OTU 4, the region of relatively low total COV is bordered by a region(s) of relatively high total COV (e.g. 600–800). Thus, all OTUs ascribed to *G. pucherani* satisfy the criteria specified for subspecies (see *Taxonomic methodology*). The lack of a high total COV interface between the low COV regions of OTUs 3 and 4 is attributed to poor sampling and the small geographic distribution of OTU 4. Assuming that *G. edouardi* is a synonym of *G. pucherani* in Table 1, and following the law of priority, OTU 3 corresponds to *G. p. verreauxi*, OTU 4 to *G. p. selateri*, OTU 5 to *G. p. pucherani*, OTU 6 to *G. p. barbata*, and OTU 7 to *G. p. edouardi*. The geographic distributions of these subspecies, and of intermediate populations, are shown in Figure 31.

The results of a cluster analysis of 704 *Numida* specimens according to characters 1–22 in Appendix 2 are summarized in Figure 12B. Nine well-defined, and one borderline OTU are recognized. The dashed line indicates the level at which eight individuals from the vicinity of Gassam, Senegal (14°50'N 15°20'W), link to form a cluster. Only 704 specimens could be analysed in this cluster analysis due to computer storage limitations. However, those specimens analysed were chosen so as to ensure uniform sampling of the sexes and collection localities. A discriminant functions analysis including all 1 245 *Numida* specimens (Fig. 32) reveals intermediate individuals between all parapatric OTUs. Therefore only one species is recognized. Following the law of priority, this species is named *Numida meleagris*.

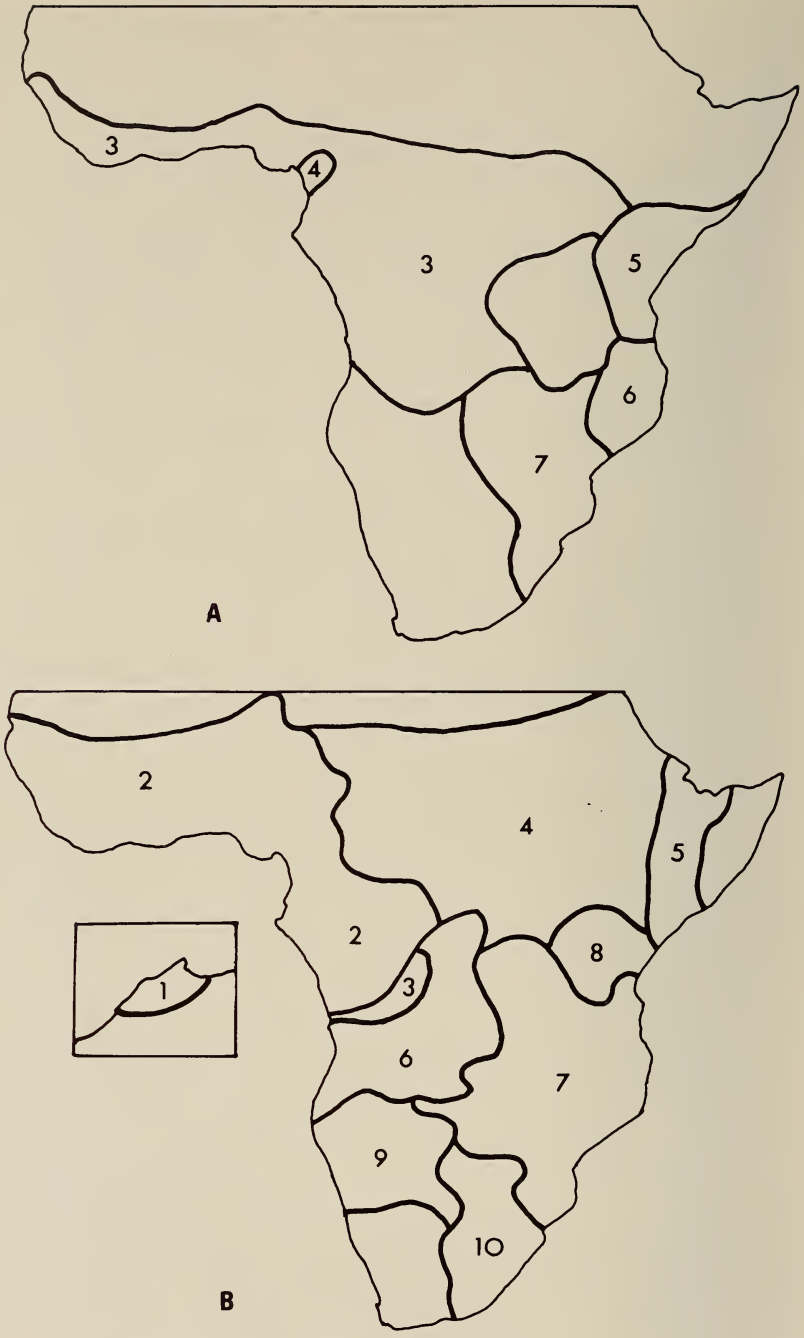


Fig. 18. The geographic distributions of OTUs comprising A. *Guttera pucherani* and B. *Numida meleagris*.

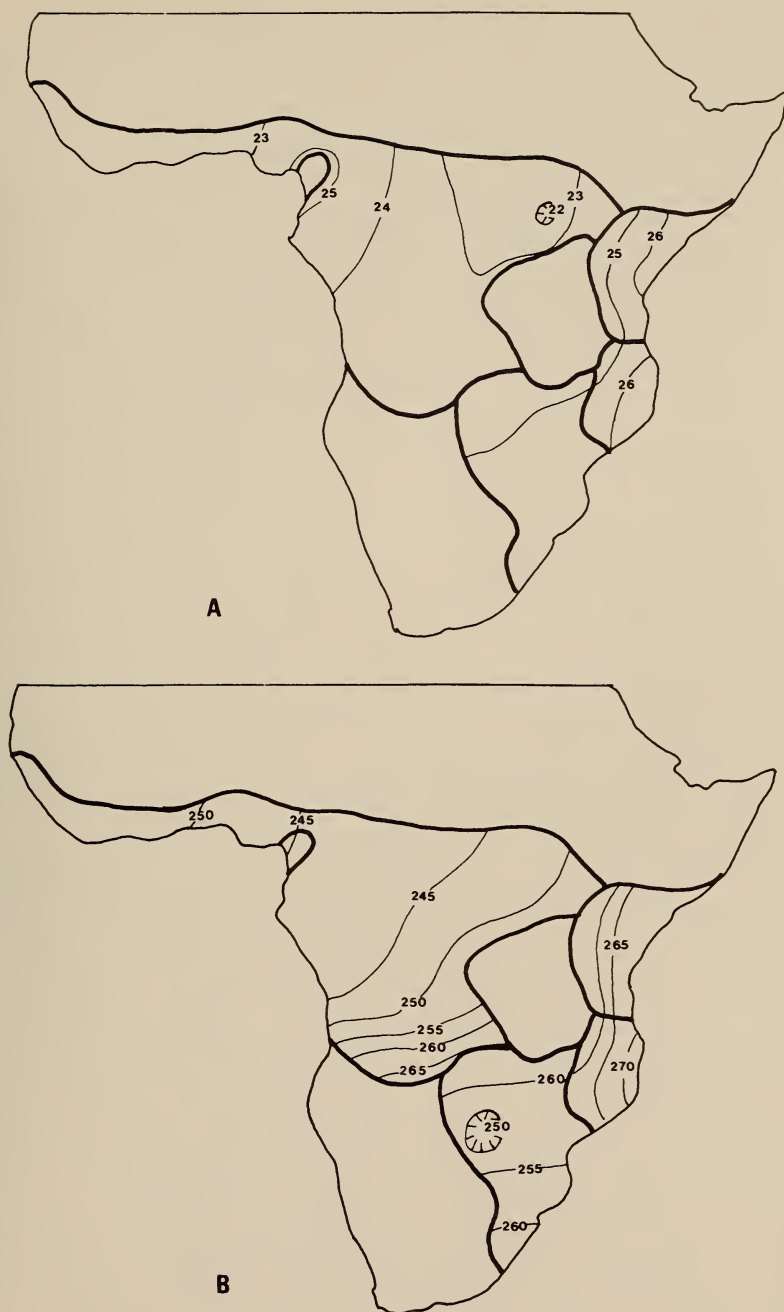


Fig. 19. Contour maps of character variation in *Guttera pucherani*. A. Bill length. B. Wing length. OTU boundaries are indicated by thick lines.

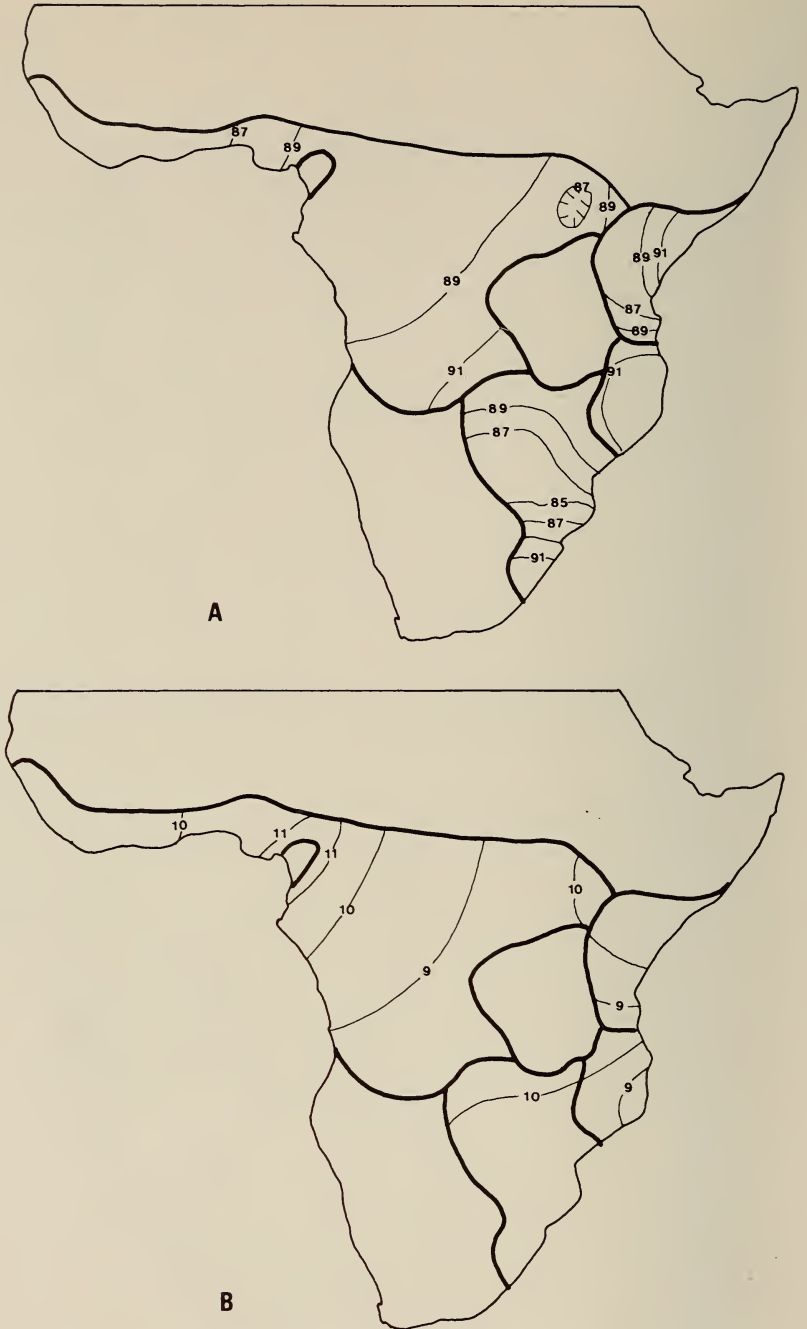


Fig. 20. Contour maps of character variation in *Guttera pucherani*. A. Tarso-metatarsus length. B. Wattle basal width. OTU boundaries are indicated by thick lines.

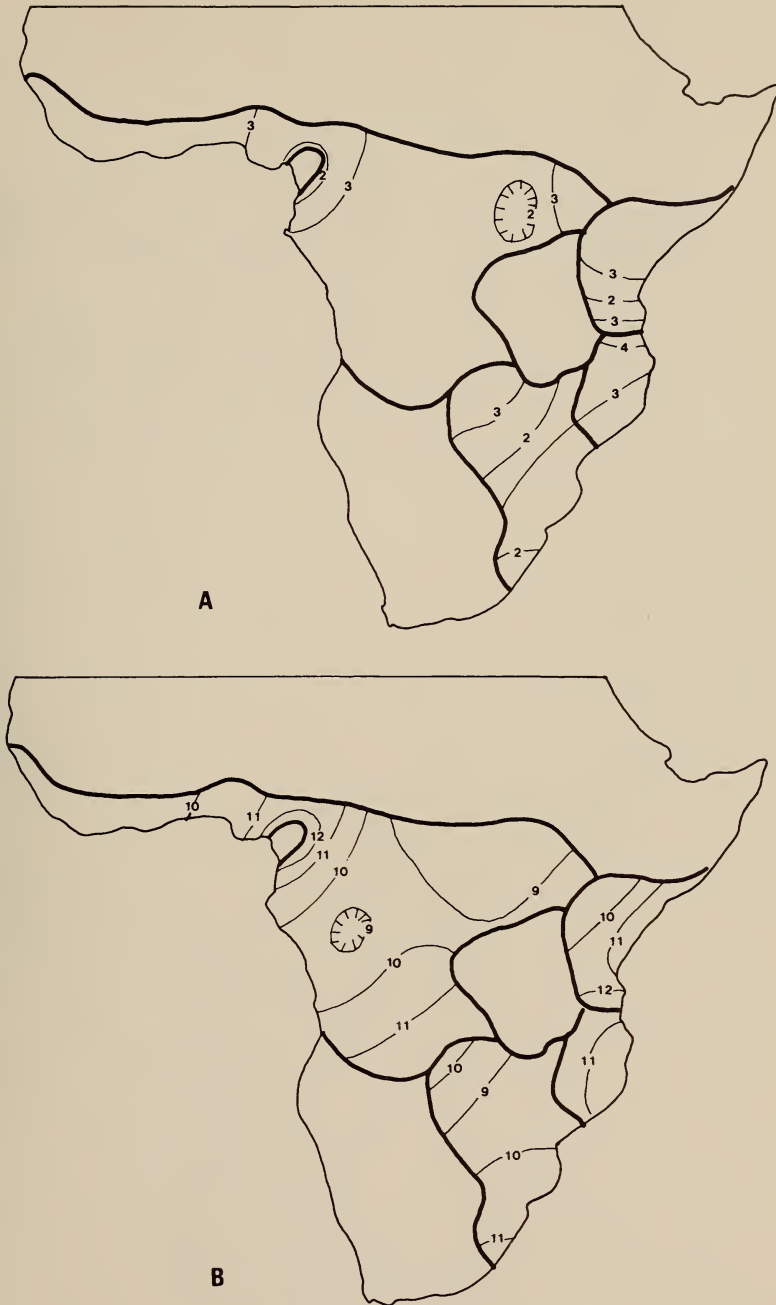


Fig. 21. Contour maps of character variation in *Guttera pucherani*. A. Wattle length.
B. dorsal spot size. OTU boundaries are indicated by thick lines.

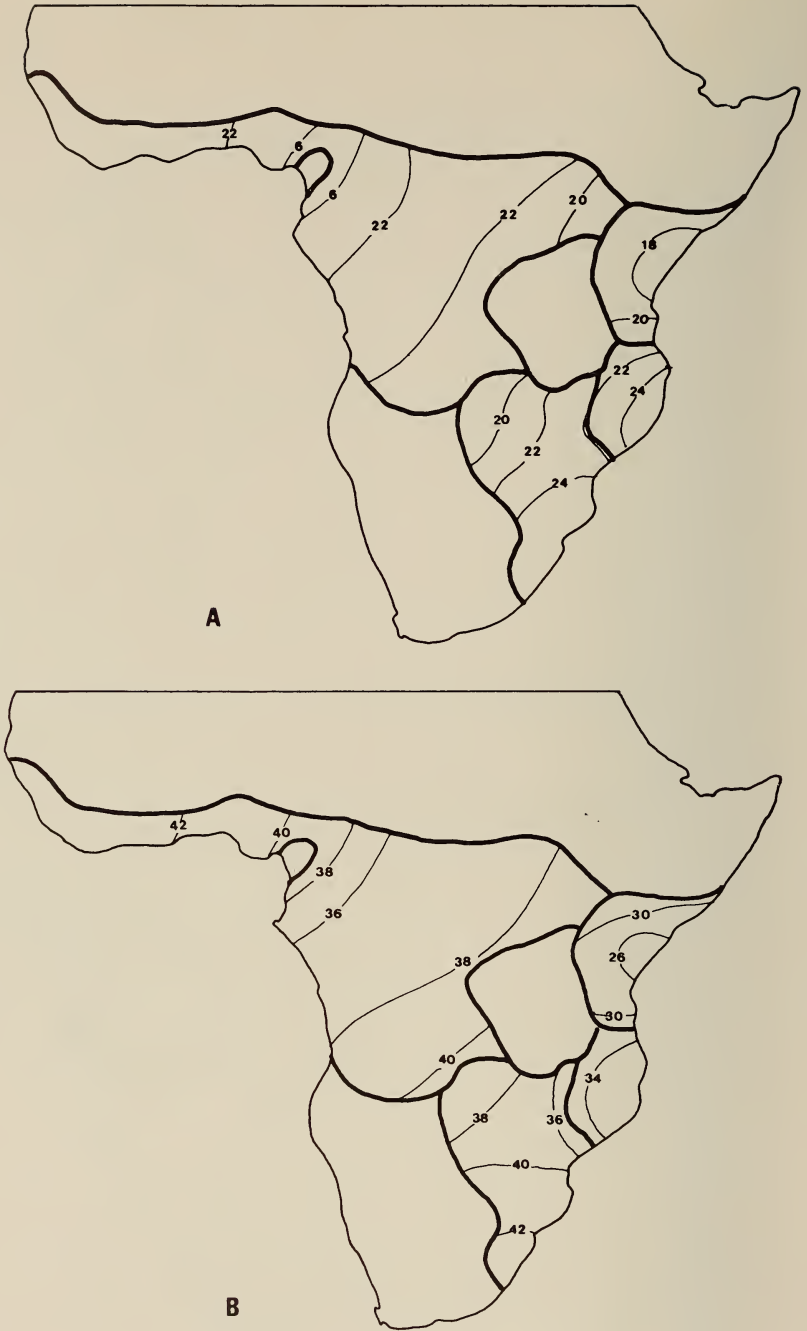


Fig. 22. Contour maps of character variation in *Guttera pucherani*. A. Crest frontal length. B. Crest rear length. OTU boundaries are indicated by thick lines.

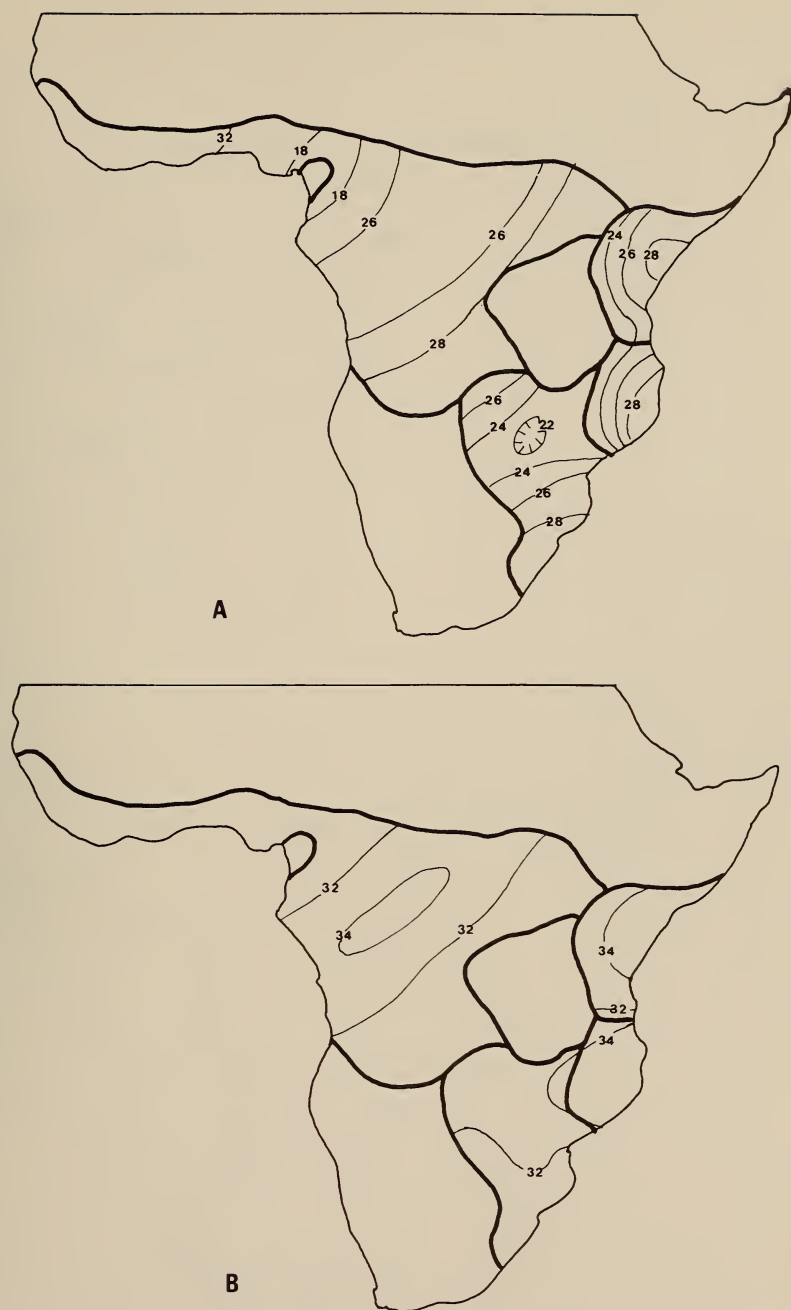


Fig. 23. Contour maps of character variation in *Guttera pucherani*. A. Crest central height. B. Crest basal length. OTU boundaries are indicated by thick lines.

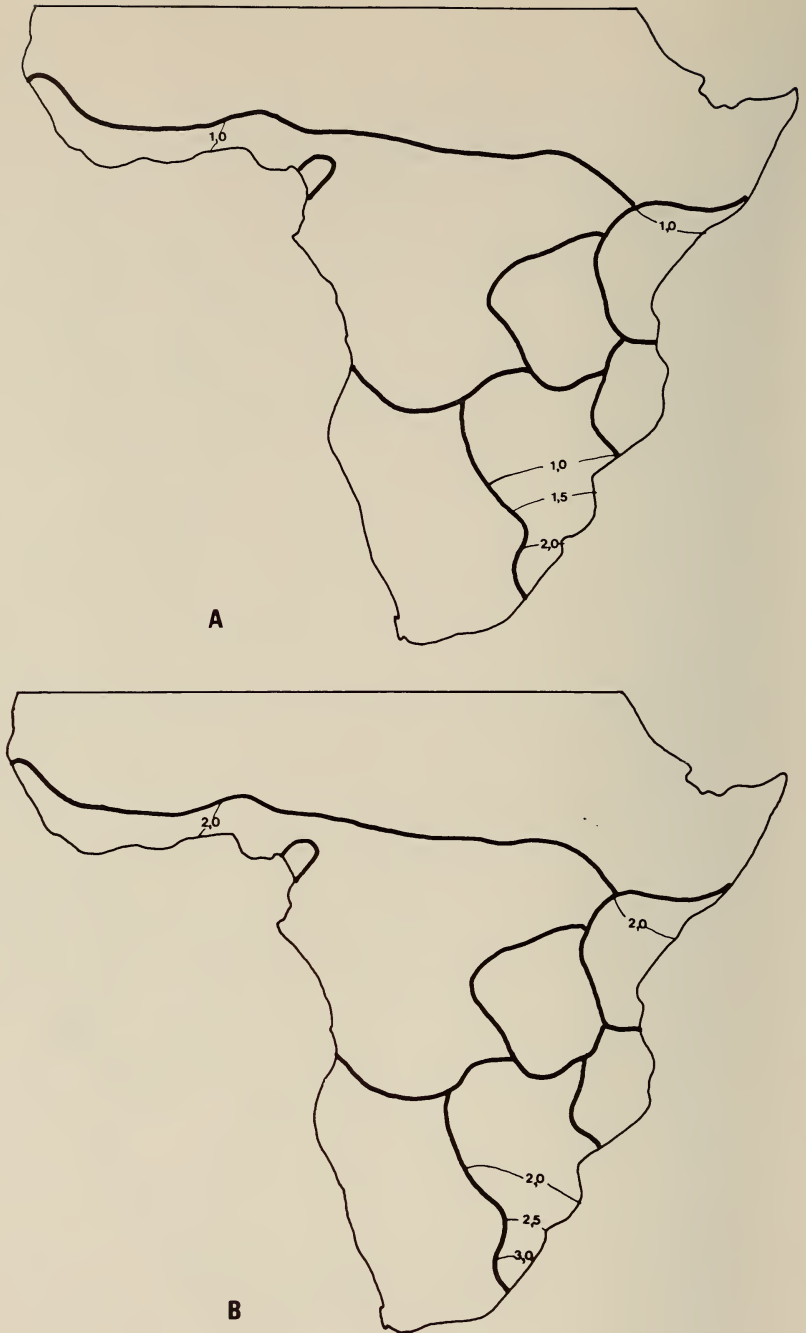


Fig. 24. Contour maps of character variation in *Guttera pucherani*. A. Anterior crest curliness. B. Posterior crest curliness. OTU boundaries are indicated by thick lines.

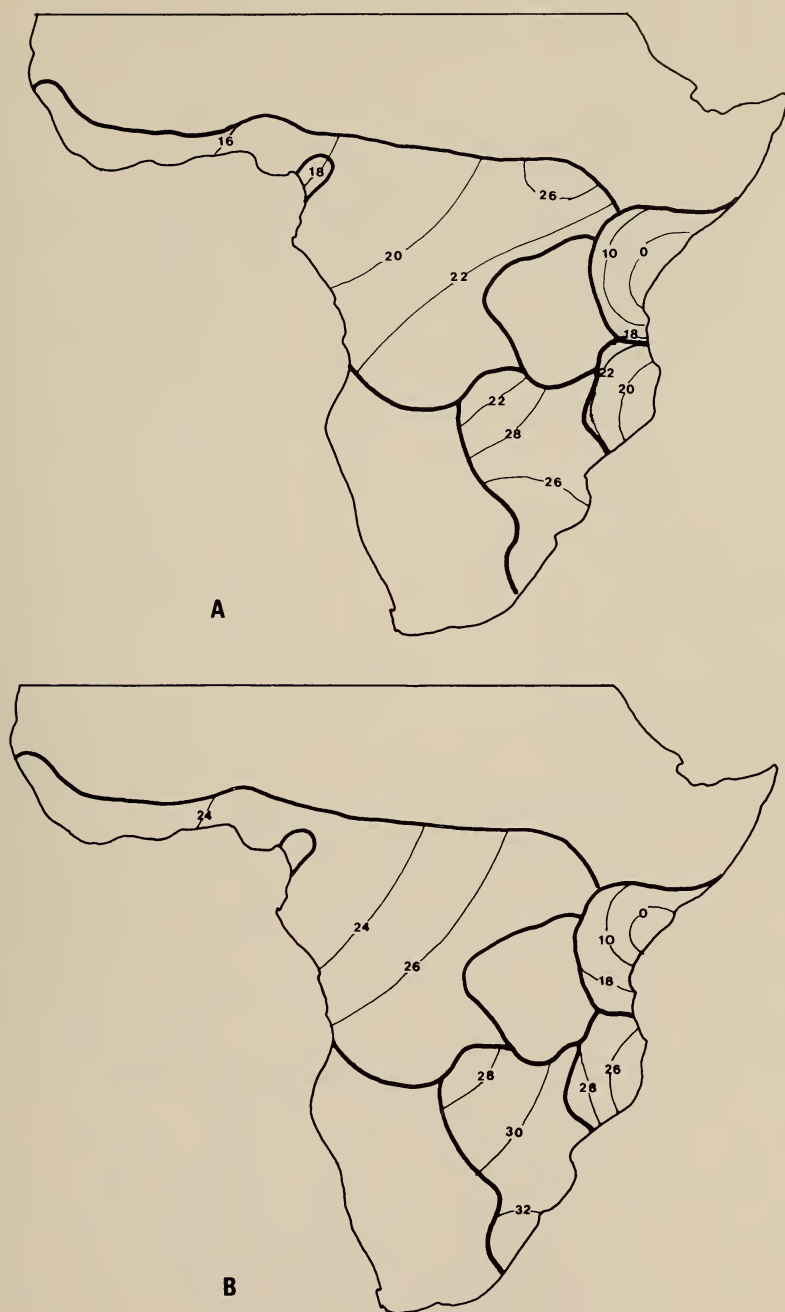


Fig. 25. Contour maps of character variation in *Guttera pucherani*. A. dorsal black collar. B. Ventral black collar. OTU boundaries are indicated by thick lines.

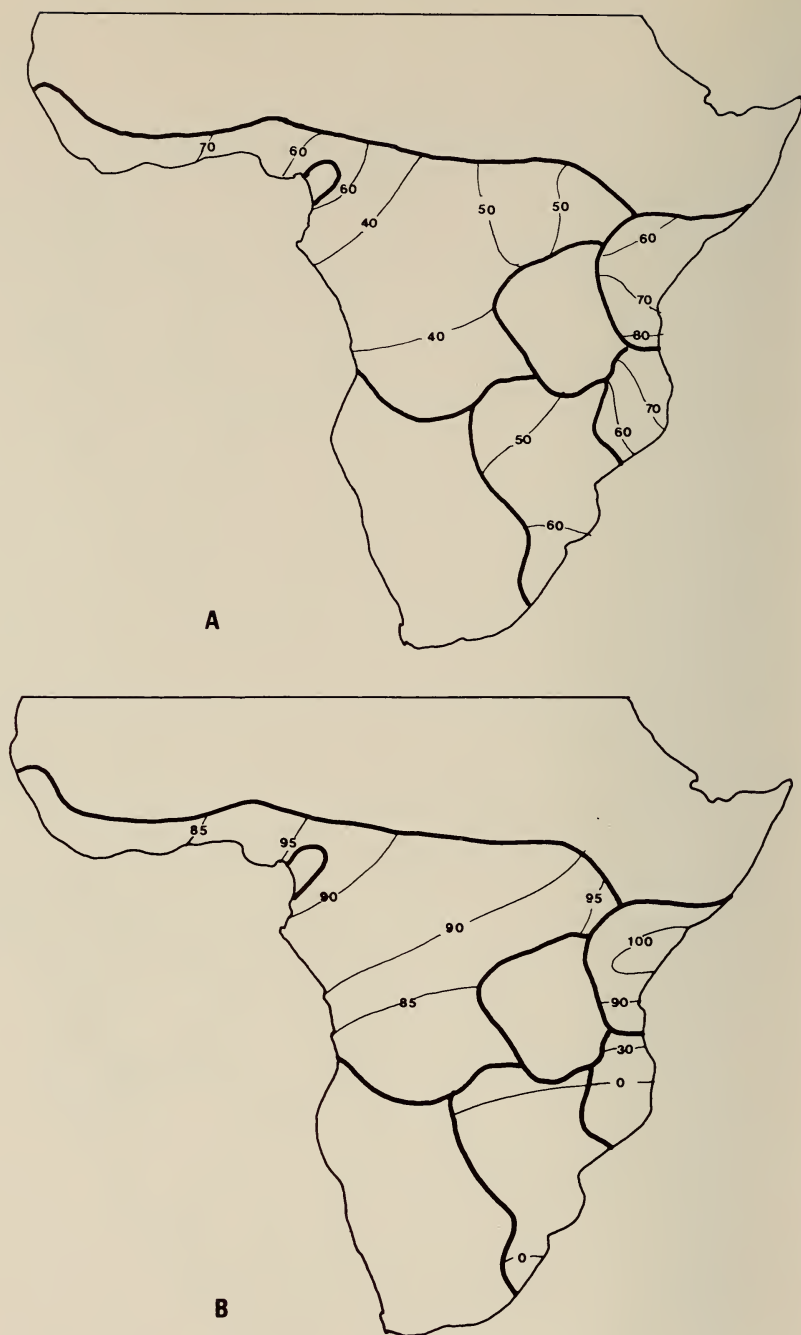


Fig. 26. Contour maps of character variation in *Guttera pucherani*. A. Occipital fold. B. Throat red. OTU boundaries are indicated by thick lines.

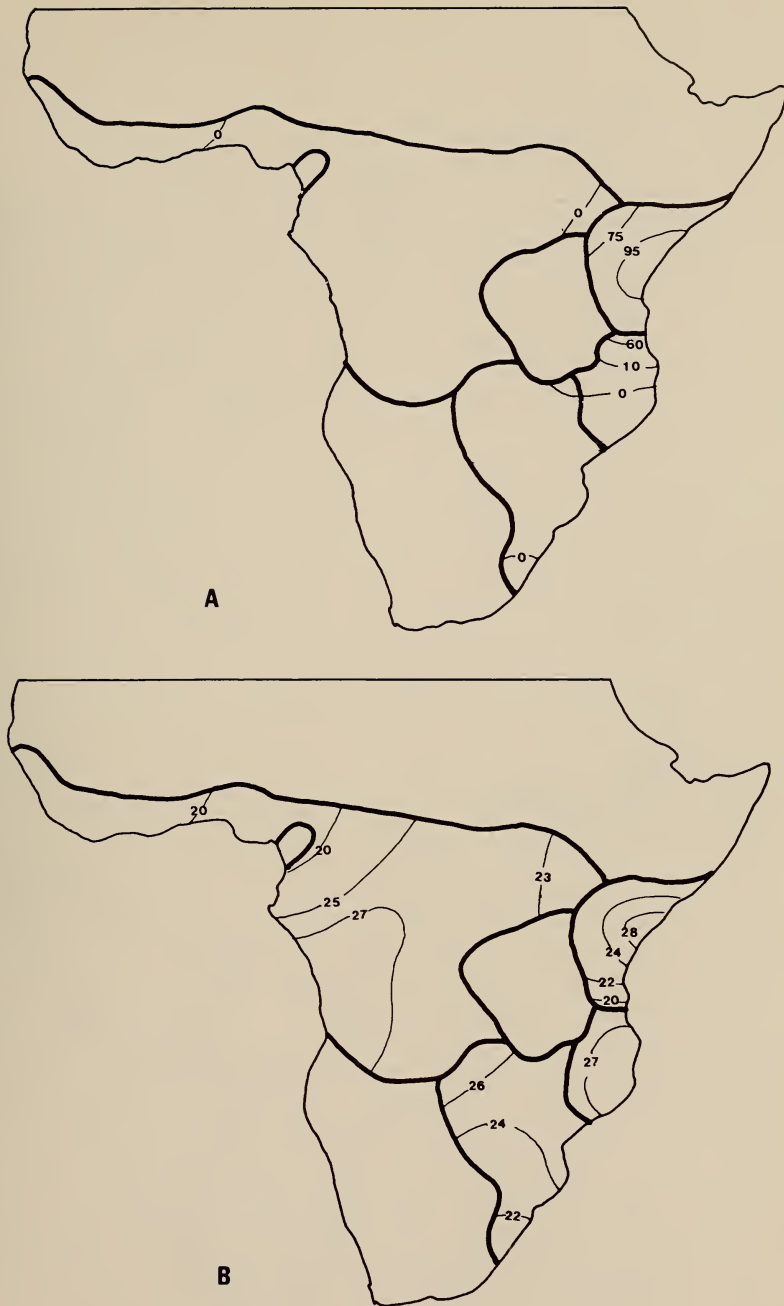


Fig. 27. Contour maps of character variation in *Guttera pucherani*. A. Orbital red. B. Dorsal spot number. OTU boundaries are indicated by thick lines.

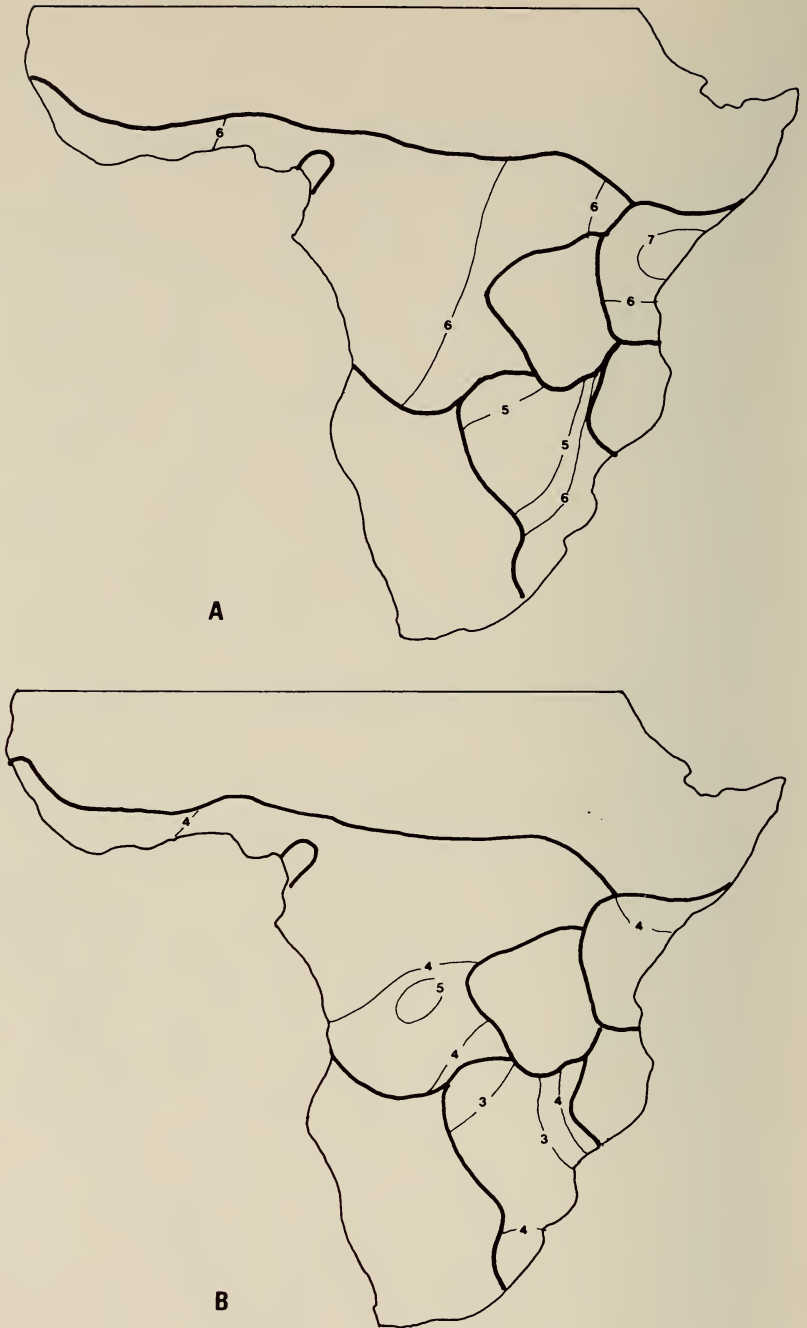


Fig. 28. Contour maps of character variation in *Guttera pucherani*. A. Total spot barbs. B. Total within spot barbs. OTU boundaries are indicated by thick lines.

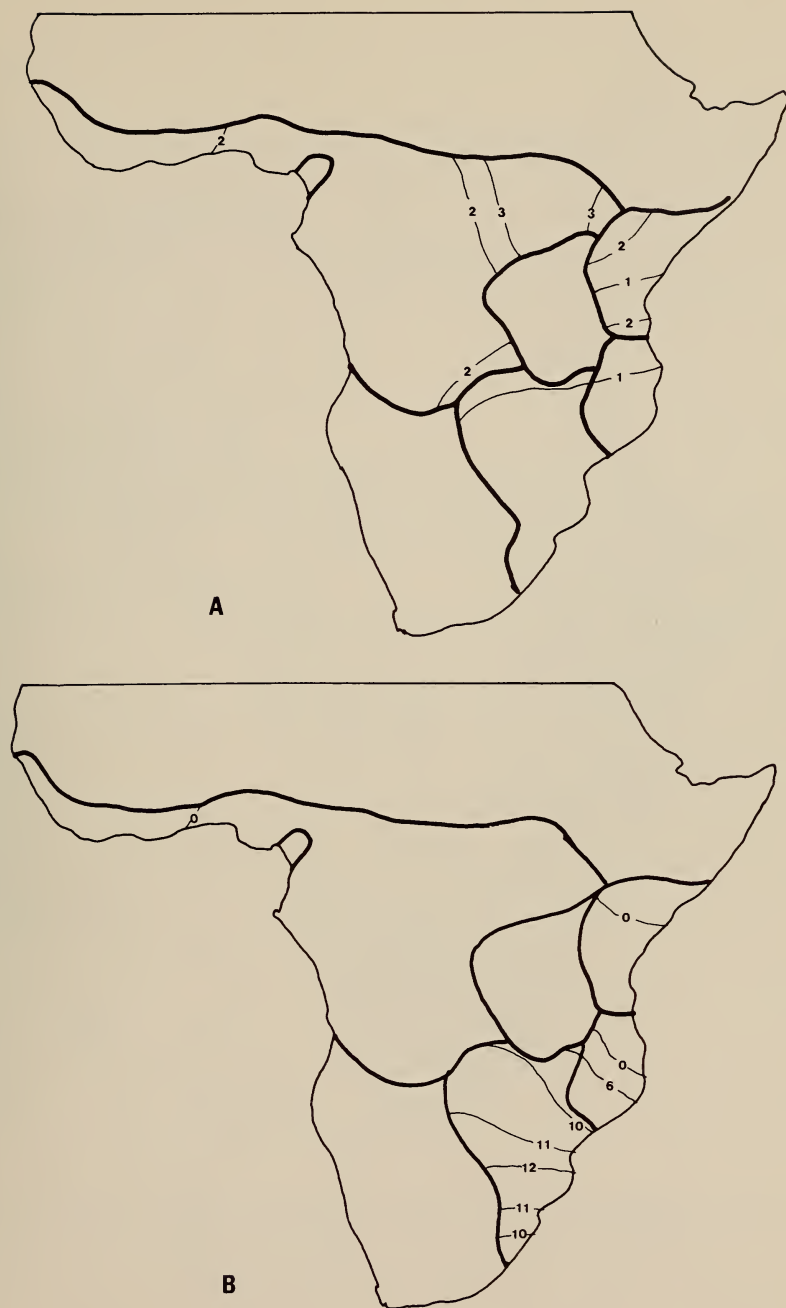


Fig. 29. Contour maps of character variation in *Guttera pucherani*. A. Spot barb blueness. B. Chestnut blotch size. OTU boundaries are indicated by thick lines.

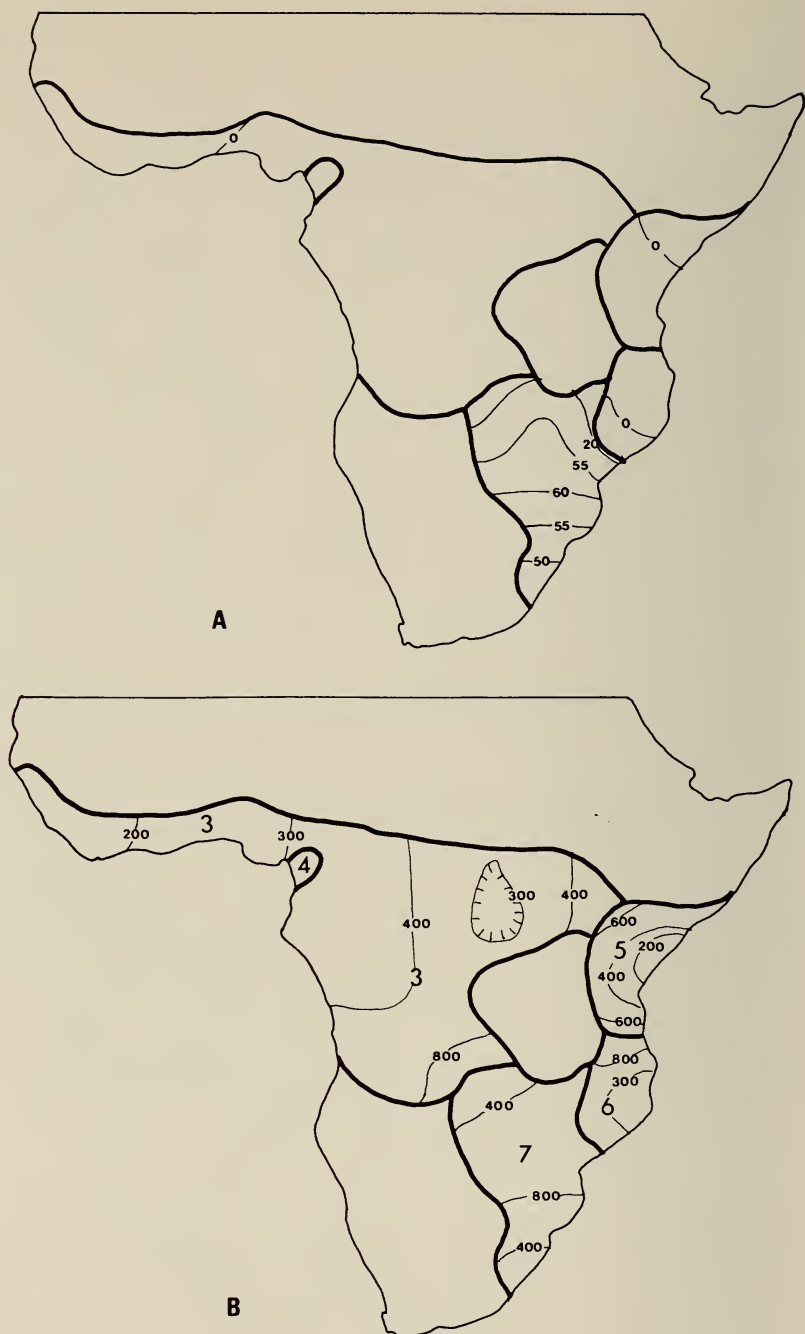


Fig. 30. Contour maps of character variation in *Guttera pucheran*. A. Chestnut blotch extent. B. Total COV. OTU boundaries are indicated by thick lines. Larger numbers in B. refer to OTU numbers shown in Figure 18A.

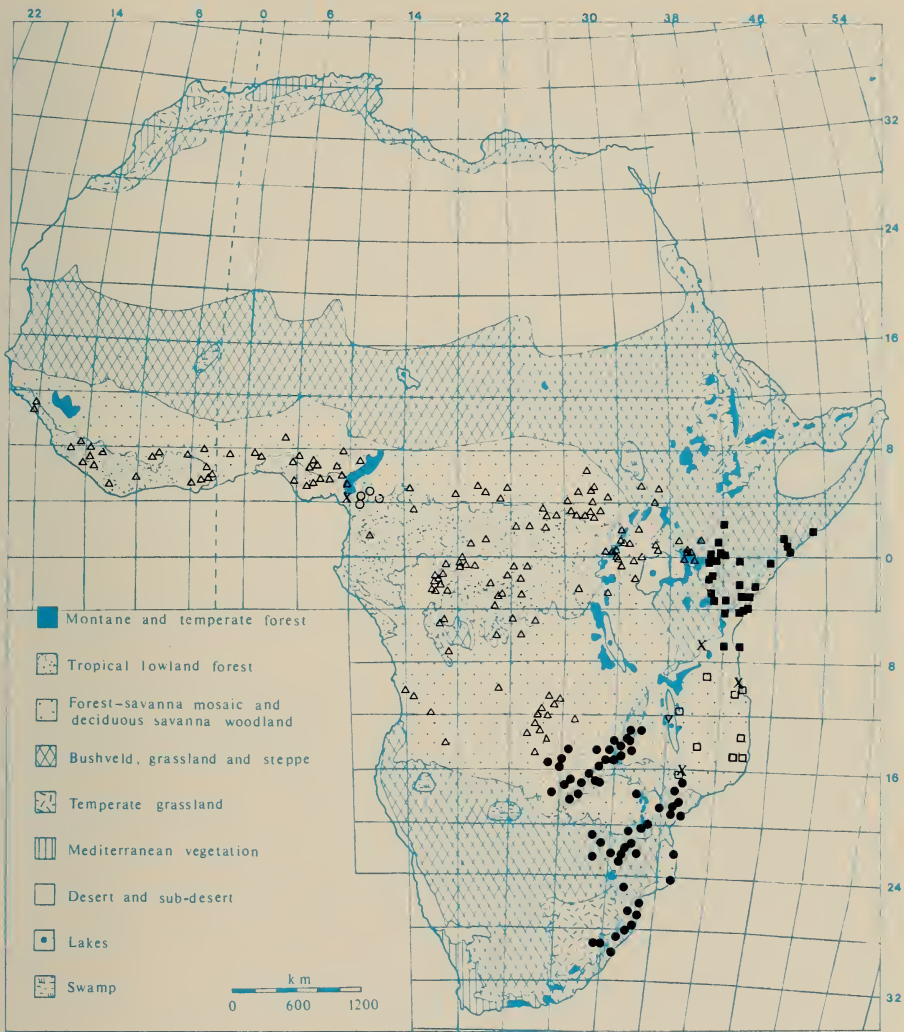


Fig. 31. The distributions of *Guttera pucherani* subspecies. *G. p. pucherani* (■), *G. p. verreauxi* (△), *G. p. sclateri* (○), *G. p. barbata* (□), *G. p. edouardi* (●). Intergrades (×).

TABLE 4

A comparison of OTU 3 for *G. pucherani* with OTUs 4, 5 and 7. × — not significantly different ($P \leq 0.05$; t test); + — OTU 3 significantly greater; — — OTU 3 significantly lower; * — differences delineate OTUs in contour maps.

Character name ¹	OTU			Contour map Figure no.
	4	5	7	
Bill length	—*	—*	—*	19A
Wing length	×	—*	—*	19B
Tarso-metatarsus length	×	×	+	20A
Wattle basal width	—*	×	—*	20B
Wattle length	+*	×	+*	21A
Dorsal spot size	—*	—*	—*	21B
Crest frontal length	+*	+*	—*	22A
Crest rear length	×	+*	×	22B
Crest central height	+*	×	×	23A
Crest basal length	×	—*	—	23B
Anterior crest curliness	×	×	—*	24A
Posterior crest curliness	×	×	—*	24B
Dorsal black collar	×	+*	—*	25A
Ventral black collar	+	+*	—*	25B
Occipital fold	—	—*	—*	26A
Throat red	×	—*	+*	26B
Orbital red	×	—*	×	27A
Dorsal spot number	+	×	×	27B
Total spot barbs	×	—*	+*	28A
Total within spot barbs	×	—	+*	28B
Spot barb blueness	+	+*	+*	29A
Chestnut blotch size	×	×	—*	29B
Chestnut blotch extent	×	×	—*	30A

¹ See Appendix 2 for character descriptions.

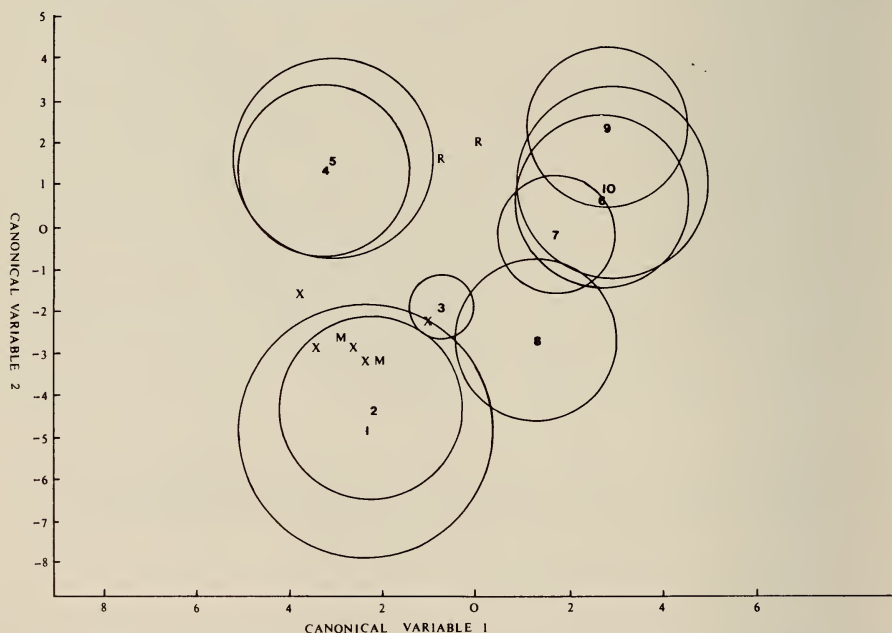


Fig. 32. A discriminant functions analysis of *Numida* OTUs. Circles encompass 90 per cent of the individuals assigned to each OTU. Only intermediate specimens between non-overlapping OTUs are plotted. M — intermediate between OTUs 4 and 7; R — intermediate between OTUs 4 and 8; X — intermediate between OTUs 4 and 2.

TABLE 5

A comparison of OTU 6 for *G. pucherani* with OTUs 5 and 7. × — not significantly different ($P \leq 0.05$; t test); + — OTU 6 significantly greater; — — OTU 6 significantly lower; * — differences delineate OTUs in contour maps.

Character name ¹	OTU		Contour map Figure no.
	5	7	
Bill length	×	×	19A
Wing length	×	+*	19B
Tarso-metatarsus length	×	+*	20A
Wattle basal width	×	—*	20B
Wattle length	×	+*	21A
Dorsal spot size	×	+*	21B
Crest frontal length	+*	×	22A
Crest rear length	+*	—*	22B
Crest central height	×	×	23A
Crest basal length	×	+*	23B
Anterior crest curliness	×	—*	24A
Posterior crest curliness	×	—*	24B
Dorsal black collar	+*	—*	25A
Ventral black collar	+*	—*	25B
Occipital fold	×	+*	26A
Throat red	—*	+	26B
Orbital red	—*	+	27A
Dorsal spot number	×	+*	27B
Total spot barbs	×	+	28A
Total within spot barbs	×	+*	28B
Spot barb blueness	—*	+	29A
Chestnut blotch size	+	—*	29B
Chestnut blotch extent	+	—*	30A

¹ See Appendix 2 for character descriptions.

The approximate geographic distributions of the ten OTUs comprising *N. meleagris* are shown in Figure 18B. Contour maps of variation in twenty-two quantitative characters analysed for this species (nos 1–22 in Appendix 2), and of the total COV for forty-eight areas (Fig. 33) are given in Figures 34–44. In these contour maps, the distributions of all ten OTUs but one, that of OTU 3, are delineated from those of their neighbours by statistically significant patterns of variation in nine to seventeen of the twenty-two characters analysed (Tables 6–11). Results of all possible pairwise statistical comparisons (t tests) between neighbouring OTUs are summarized in Tables 6–11. The distribution of OTU 3, the borderline OTU in Figure 11B, is delineated from those of its neighbours (OTUs 2 and 6) by at most two characters (Tables 7, 9). In the contour map of total COV (Fig. 45), the distribution of all OTUs, except again OTU 3, enclose a region of relatively low total COV (*c.* 400–500) bordered by a region(s) of relatively high total COV (*c.* 700–1000). Thus, all OTUs ascribed to *N. meleagris*, except OTU 3, satisfy the criteria set for subspecies (see *Taxonomic methodology*). In Table 1, following the law of priority, OTU 1 corresponds to *N. m. sabyi*, OTU 2 to *N. m. galeata*, OTU 4 to *N. m. meleagris*, OTU 5 to *N. m. somalienses*, OTU 6 to *N. m. marungensis*, OTU 7 to *N. m. mitrata*, OTU 8 to *N. m. reichenowi*, OTU 9 to *N. m. damarensis*, and OTU 10 to *N. m. coronata*.



Fig. 33. Areas used in contour map analysis of *Numida meleagris*.

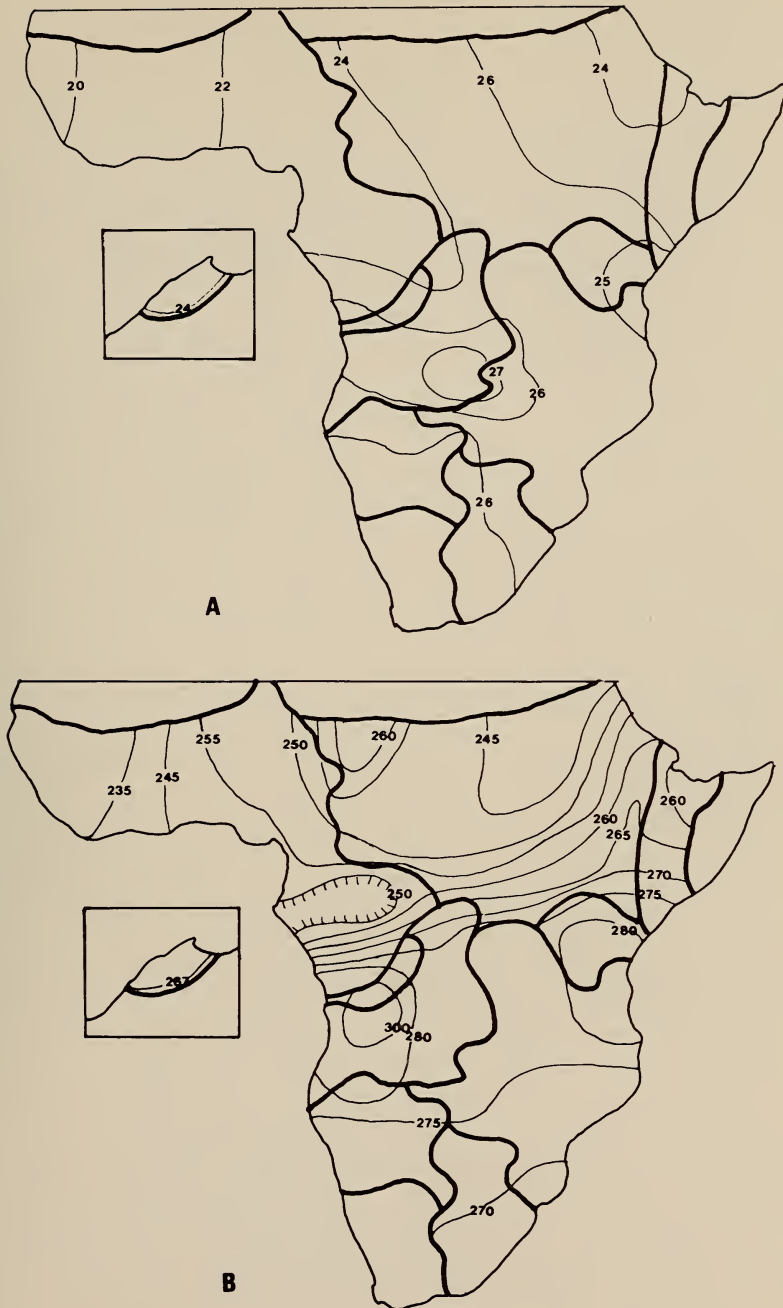


Fig. 34. Contour maps of character variation in *Numida meleagris*. A. Bill length. B. Wing length. OTU boundaries are indicated by thick lines.

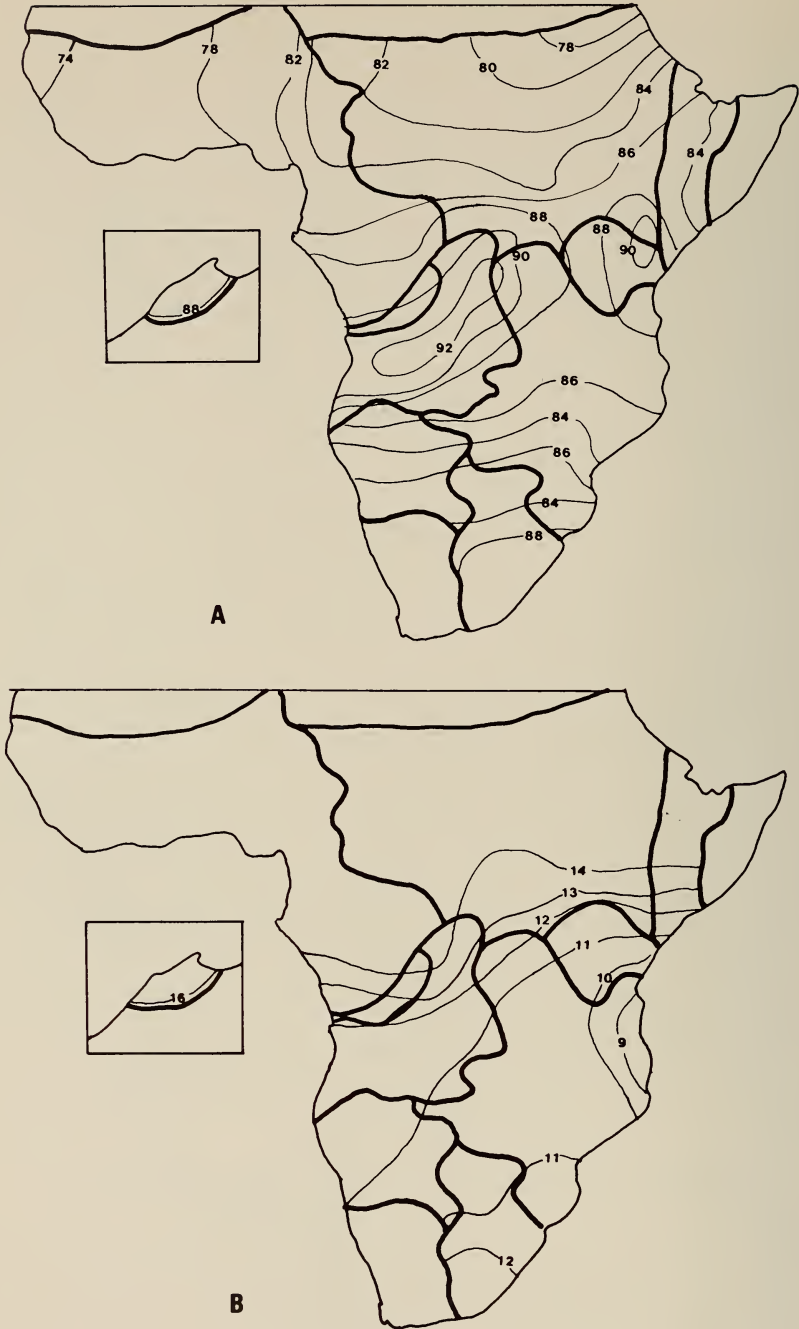


Fig. 35. Contour maps of character variation in *Numida meleagris*. A. Tarso-metatarsus length. B. Wattle basal width. OTU boundaries are indicated by thick lines.

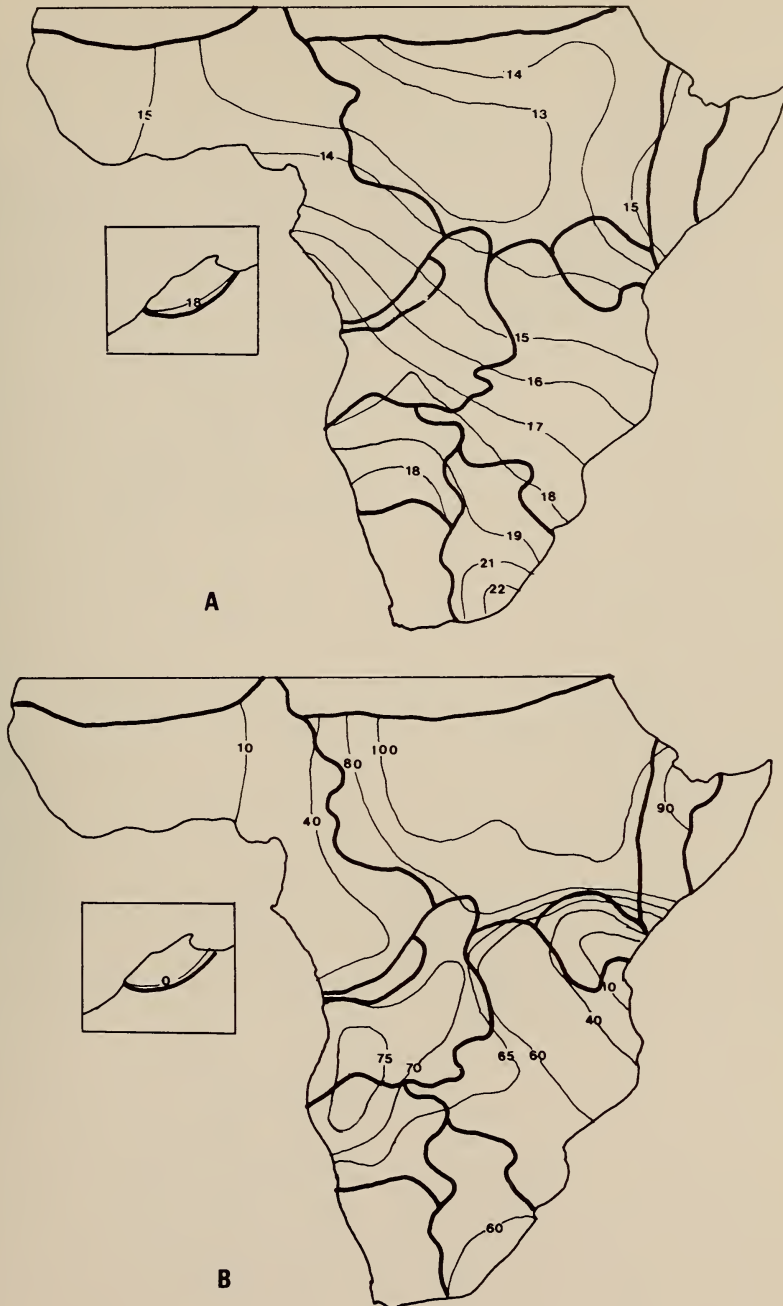


Fig. 36. Contour maps of character variation in *Numida meleagris*. A. Wattle length. B. Wattle per cent blue. OTU boundaries are indicated by thick lines.

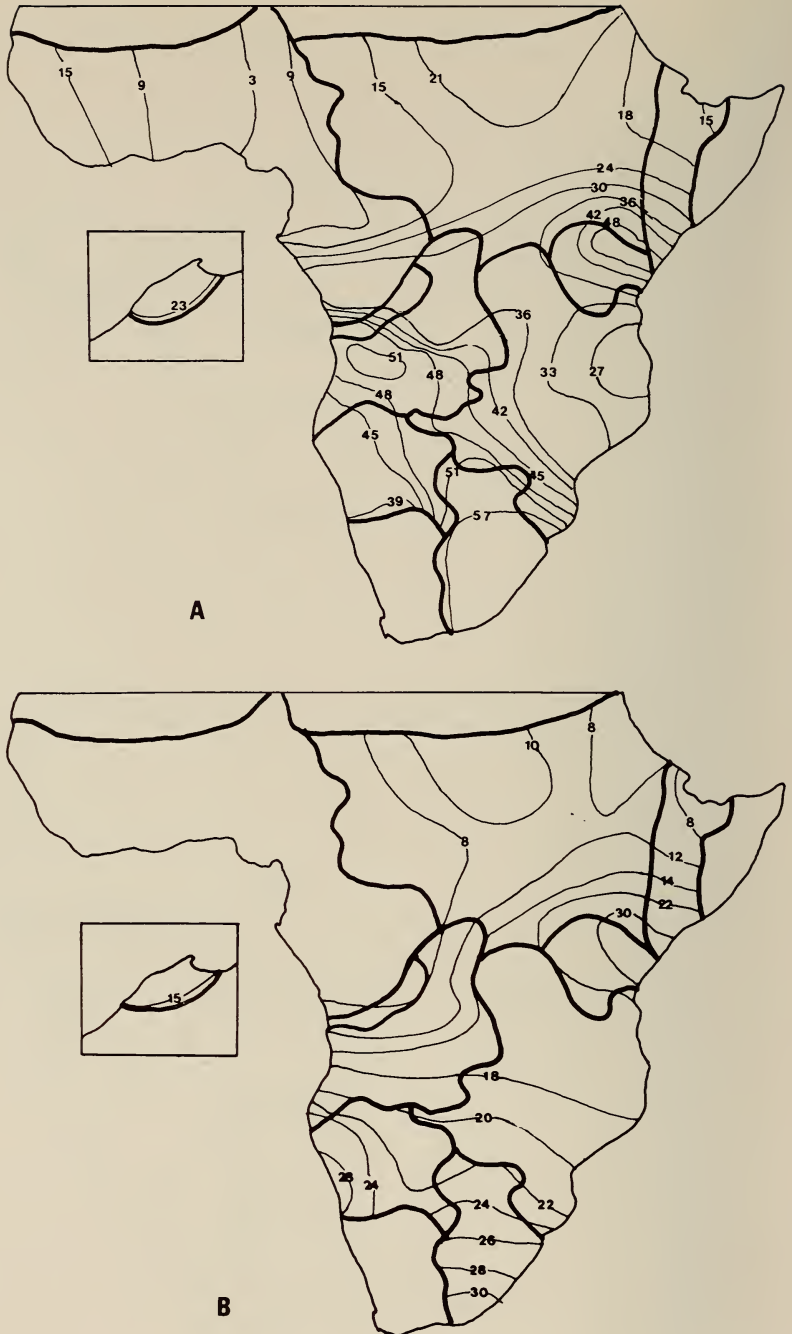


Fig. 37. Contour maps of character variation in *Numida meleagris*. A. Helmet frontal length. B. Helmet rear length. OTU boundaries are indicated by thick lines.

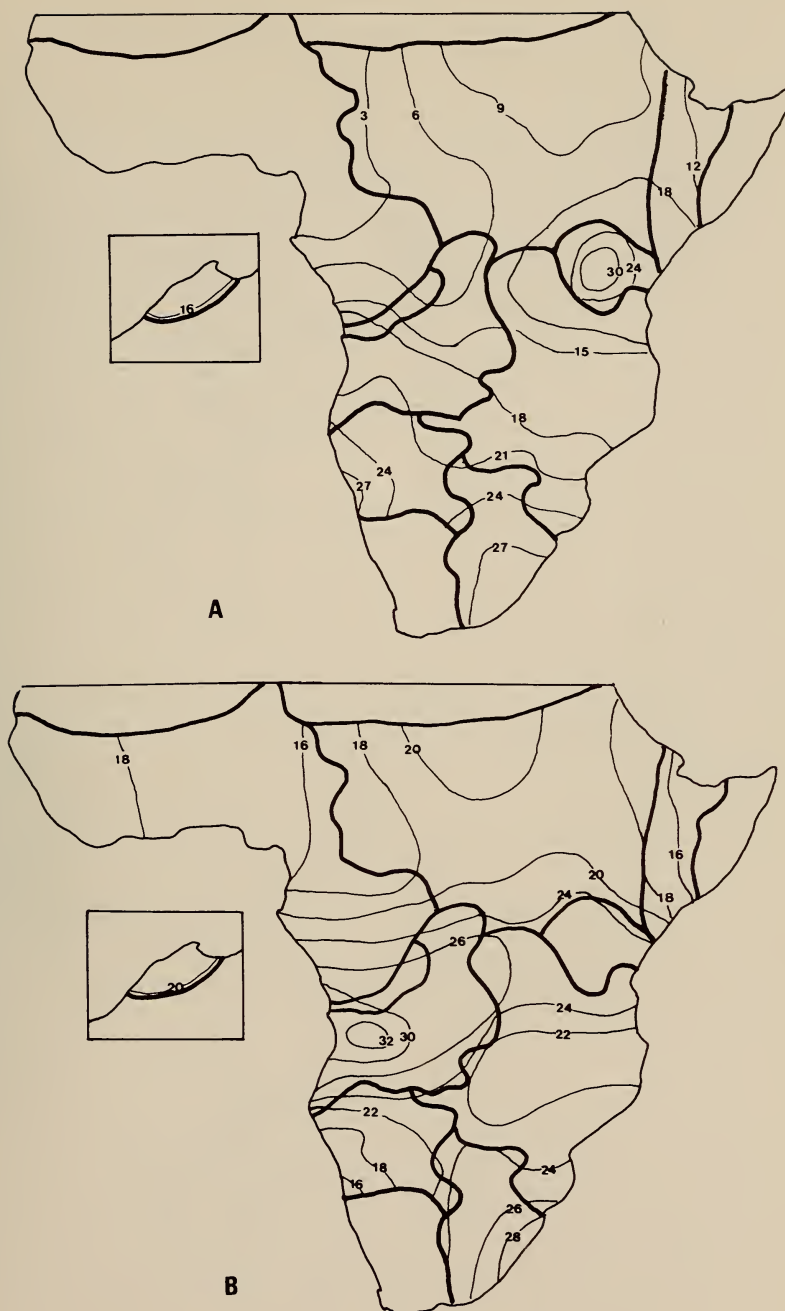


Fig. 38. Contour maps of character variation in *Numida meleagris*. A. Helmet central height. B. Helmet basal length. OTU boundaries are indicated by thick lines.

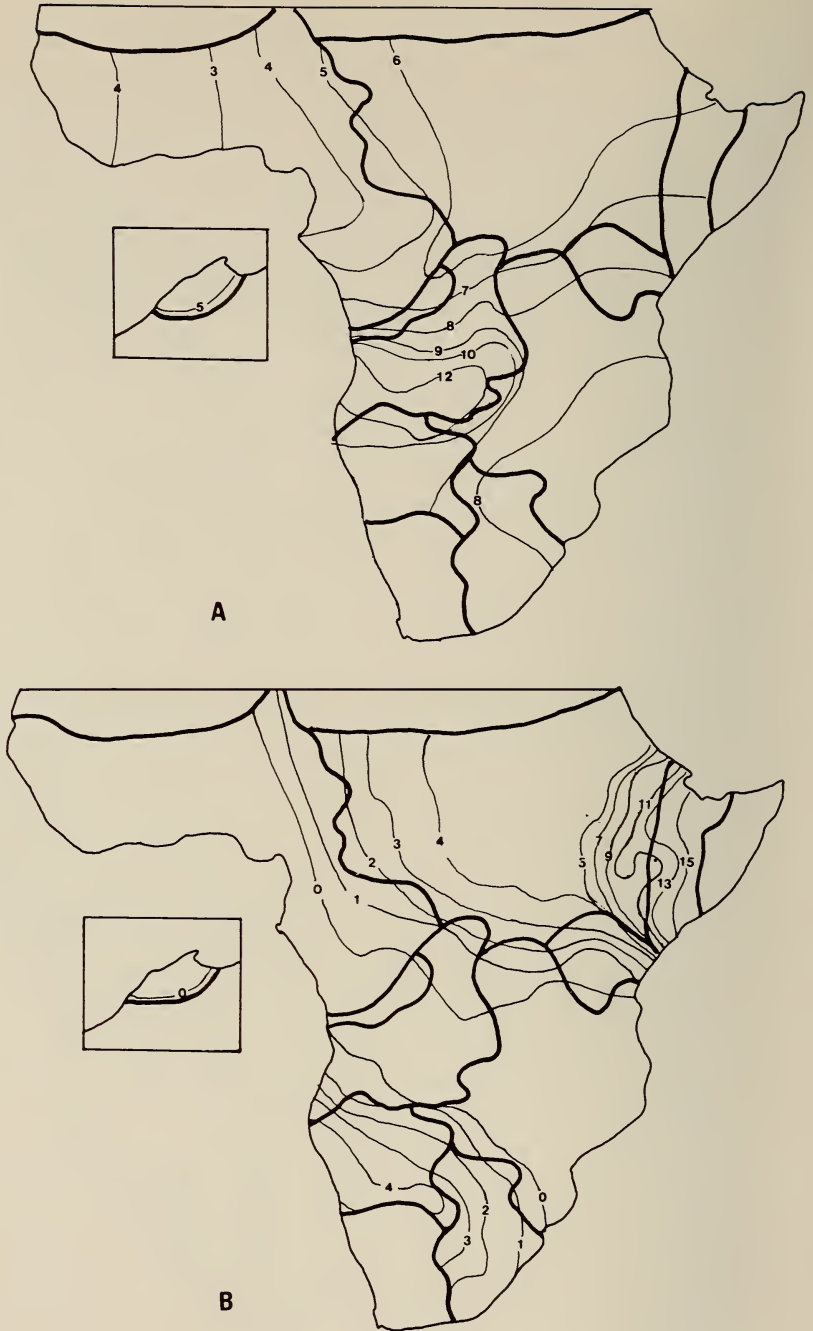


Fig. 39. Contour maps of character variation in *Numida meleagris*. A. Helmet thickness. B. Cere structure length. OTU boundaries are indicated by thick lines.

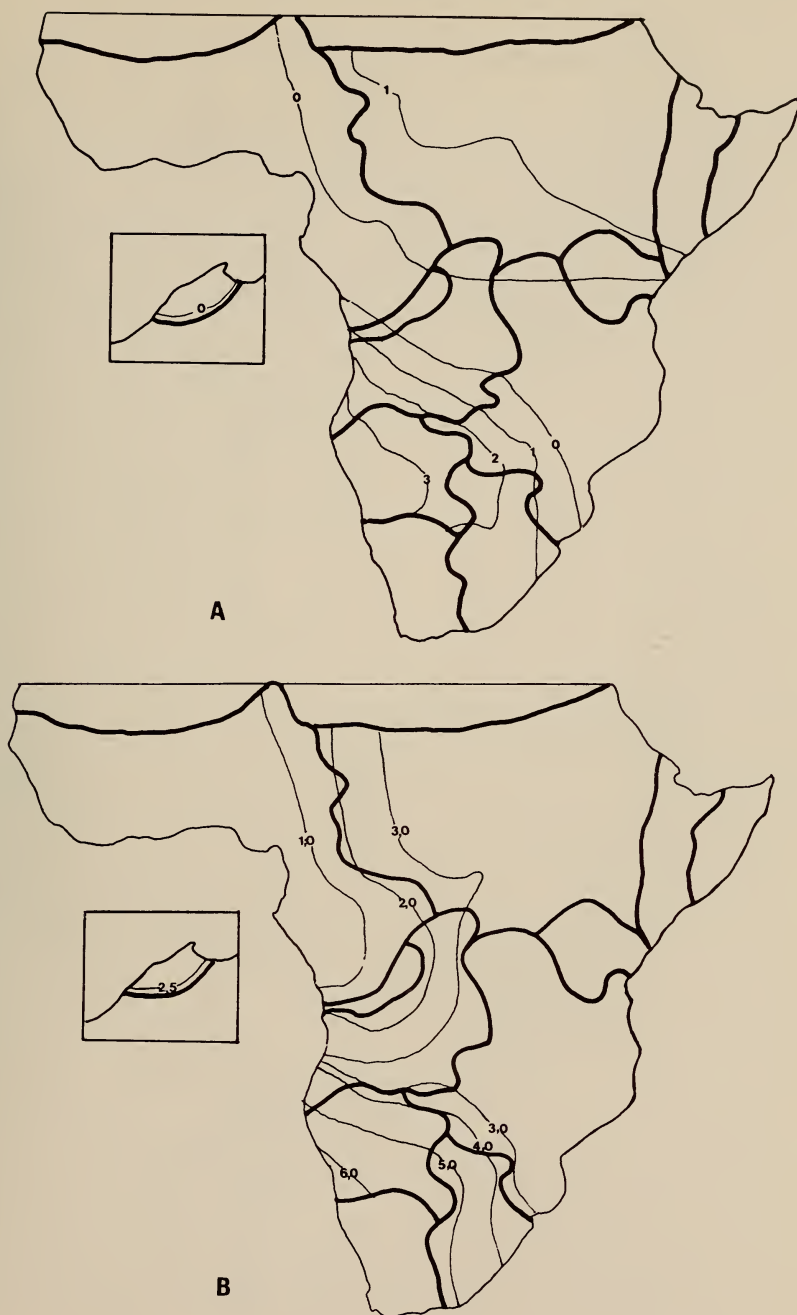


Fig. 40. Contour maps of character variation in *Numida meleagris*. A. Cere structure thickness. B. Collar plumage. OTU boundaries are indicated by thick lines.

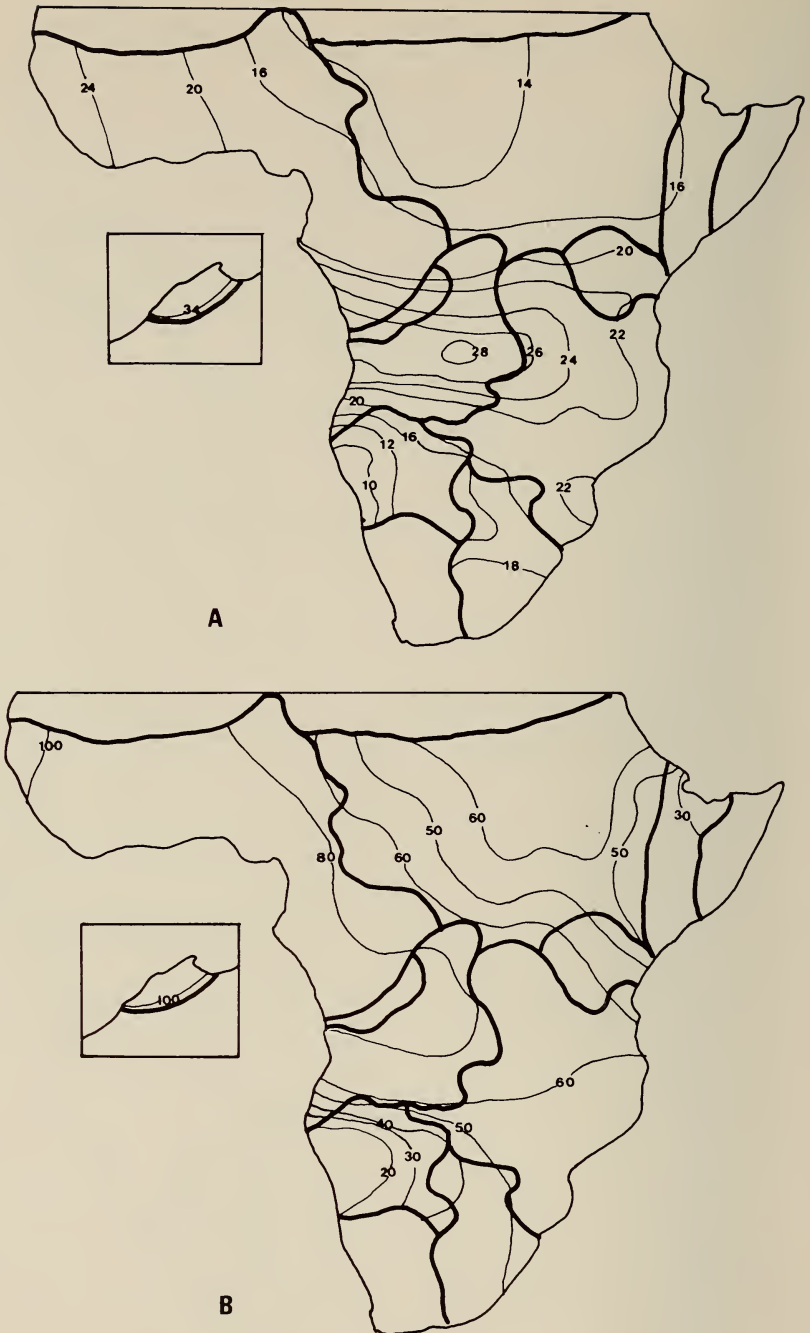


Fig. 41. Contour maps of character variation in *Numida meleagris*. A. Nape filoplume length. B. Nape anteroposterior coverage. OTU boundaries are indicated by thick lines.

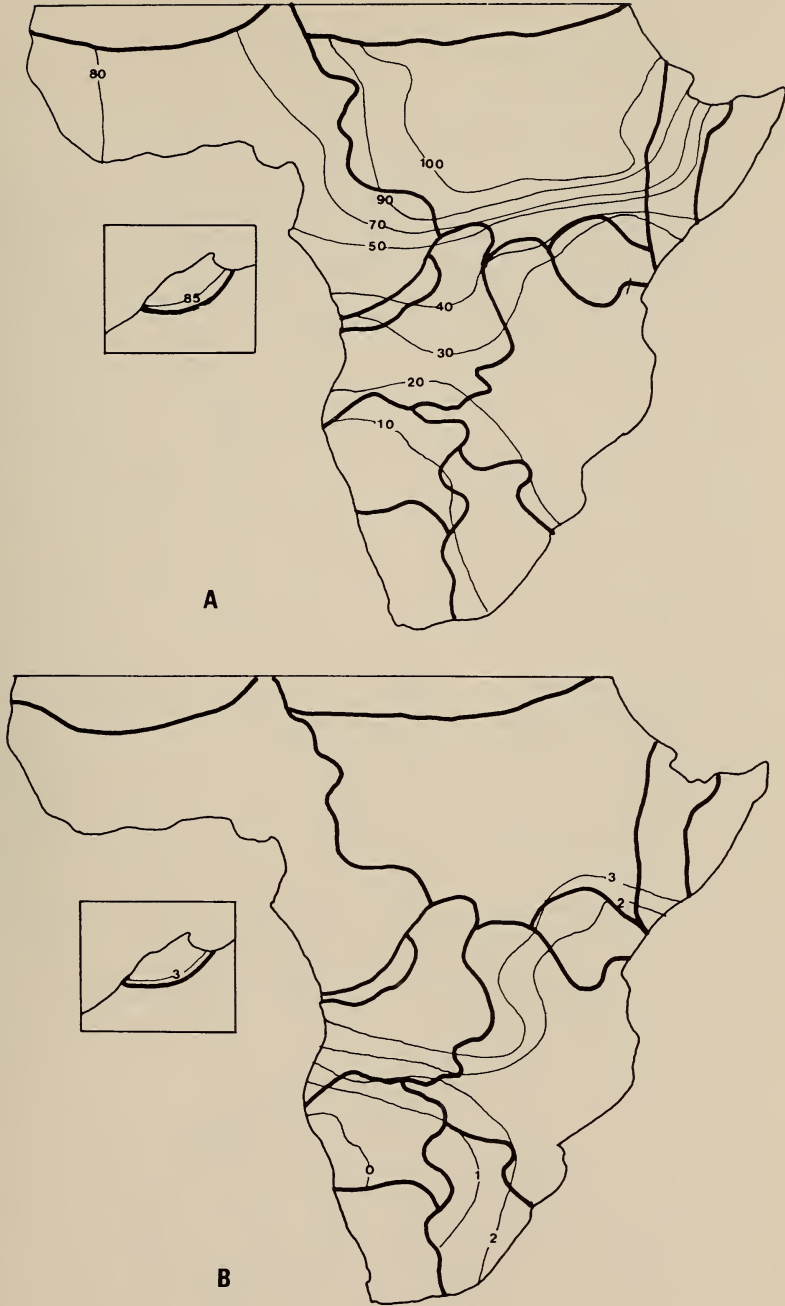


Fig. 42. Contour maps of character variation in *Numida meleagris*. A. Nape filoplume lateral coverage. B. Nape filoplume density. OTU boundaries are indicated by thick lines.

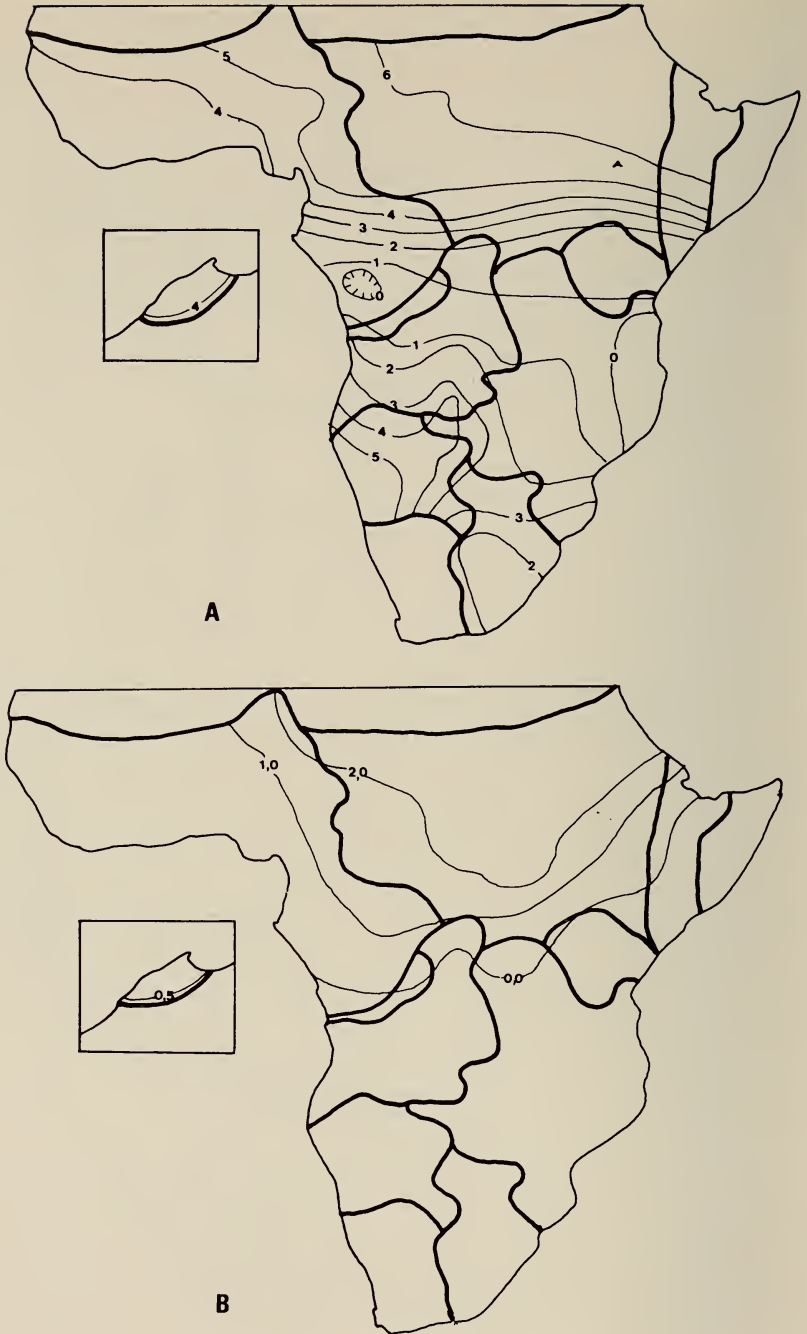


Fig. 43. Contour maps of character variation in *Numida meleagris*. A. Secondary remex outer web vermiculation. B. Wing covert barring. OTU boundaries are indicated by thick lines.

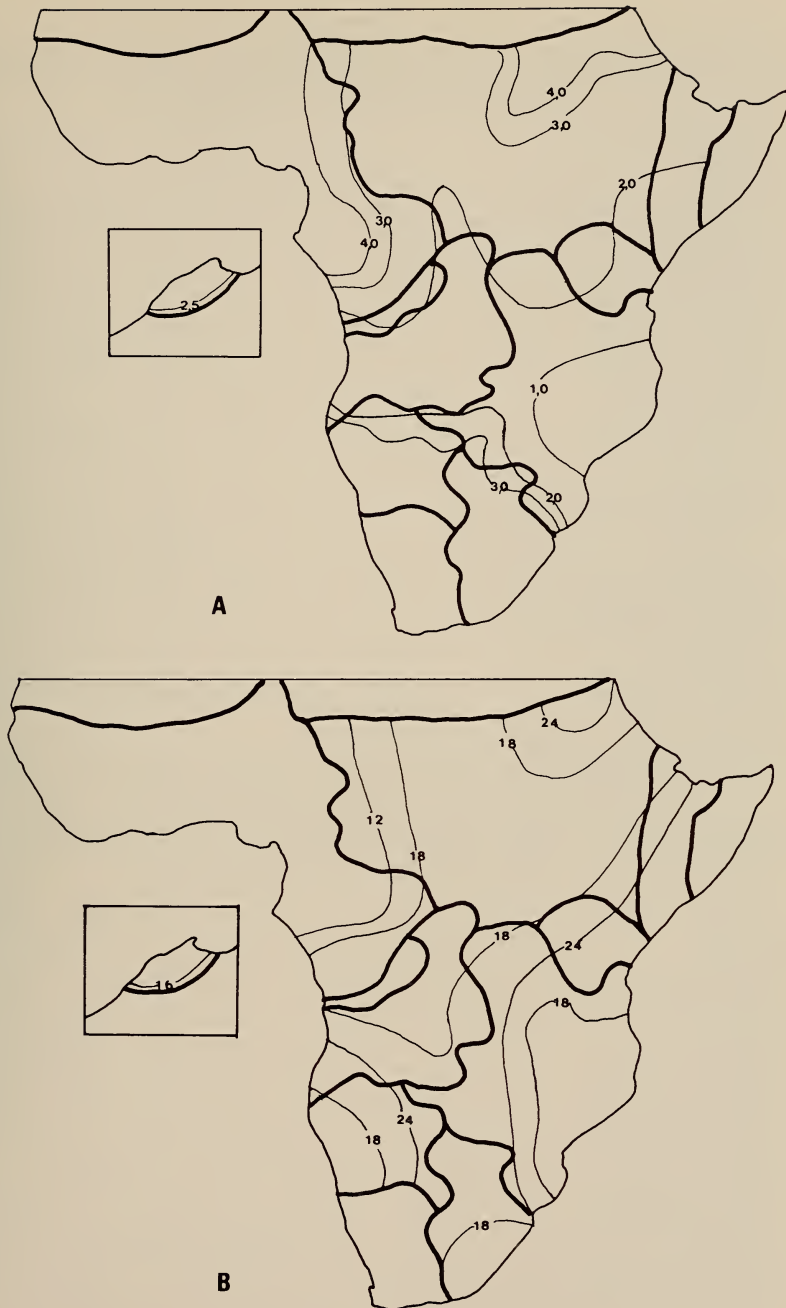


Fig. 44. Contour maps of character variation in *Numida meleagris*. A. Dorsal vermiculation. B. Dorsal spot size. OTU boundaries are indicated by thick lines.

TABLE 6

A comparison of OTU 4 for *N. meleagris* with OTUs 2, 5, 6, 7 and 8. × — not significantly different ($P \leq 0,05$; t test); + — OTU 4 significantly greater; — — OTU 4 significantly lower; * — differences delineate OTUs in contour maps.

Character name ¹	OTU					Contour map Figure no.
	2	5	6	7	8	
Bill length	+*	×	—*	—	×	34A
Wing length	+	×	—*	—*	—*	34B
Tarso-metatarsus length	+*	×	—*	—	—*	35A
Wattle basal width	×	×	+*	+*	+*	35B
Wattle length	—	—*	—*	—*	+	36A
Wattle per cent blue	+*	+*	+*	+*	+*	36B
Helmet frontal length	+*	×	—*	—*	—*	37A
Helmet rear length	+*	×	—	—	—*	37B
Helmet central height	+*	×	—	—*	—*	38A
Helmet basal length	×	+*	—*	—*	—*	38B
Helmet thickness	+*	×	—*	—*	—	39A
Cere structure length	+*	—*	+*	+*	+	39B
Cere structure thickness	+*	×	+*	+*	+*	40A
Collar plumage	+*	×	×	—	×	40B
Nape filoplume length	—*	—*	—*	—*	—*	41A
Nape filoplume anteroposterior coverage	—*	+*	—*	×	×	41B
Nape filoplume lateral coverage	+*	+*	+*	+*	+*	42A
Nape filoplume density	×	×	×	+	+*	42B
Secondary remex outer web vermiculation	+*	+	+*	+*	+*	43A
Wing covert barring	+*	+*	+*	+*	+*	43B
Dorsal vermiculation	—*	+	+*	+*	+	44A
Dorsal spot size	+*	—*	—	×	—*	44B

¹ See Appendix 2 for character descriptions.

TABLE 7

A comparison of OTU 2 for *N. meleagris* with OTUs 1, 3 and 6. × — not significantly different ($P \leq 0,05$; t test); + — OTU 2 significantly greater; — — OTU 2 significantly lower; * — differences delineate OTUs in contour maps.

Character name ¹	OTUs			Contour map Figure no.
	1	3	6	
Bill length	×	—	—*	34A
Wing length	—*	—	—*	34B
Tarso-metatarsus length	—*	—	—*	35A
Wattle basal width	×	×	+*	35B
Wattle length	×	×	—	36A
Wattle per cent blue	+*	—*	—*	36B
Helmet frontal length	—*	—	—*	37A
Helmet rear length	—*	—	—	37B
Helmet central height	—*	—	—	38A
Helmet basal length	×	—	—*	38B
Helmet thickness	×	—	—*	39A
Cere structure length	×	+	×	39B
Cere structure thickness	×	+	×	40A
Collar plumage	—*	—*	—*	40B
Nape filoplume length	—*	×	—*	41A
Nape filoplume anteroposterior coverage	×	×	+	41B
Nape filoplume lateral coverage	×	+	+	42A
Nape filoplume density	×	×	×	42B
Secondary remex outer web vermiculation	×	+	+	43A
Wing covert barring	+*	+	+*	43B
Dorsal vermiculation	+*	+	+*	44A
Dorsal spot size	+*	—	—	44B

¹ See Appendix 2 for character descriptions.

TABLE 8

A comparison of OTU 8 for *N. meleagris* with OTUs 5 and 7. × — not significantly different; ($P \leq 0.05$; t test); + — OTU 8 significantly greater; — — OTU 8 significantly lower; * — differences delineate OTUs in contour maps.

Character name ¹	OTUs		Contour map Figure no.
	5	7	
Bill length	×	—*	34A
Wing length	+*	+*	34B
Tarso-metatarsus length	+*	+*	35A
Wattle basal width	—	+	35B
Wattle length	—	—	36A
Wattle per cent blue	—*	—*	36B
Helmet frontal length	+*	+*	37A
Helmet rear length	+*	+*	37B
Helmet central height	+*	+*	38A
Helmet basal length	+*	+*	38B
Helmet thickness	+	+	39A
Cere structure length	—*	+	39B
Cere structure thickness	—	+	40A
Collar plumage	×	—	40B
Nape filoplume length	+*	—*	41A
Nape filoplume anteroposterior coverage	+	×	41B
Nape filoplume lateral coverage	—	+	42A
Nape filoplume density	—*	×	42B
Secondary remex outer web vermiculation	—*	+*	43A
Wing covert barring	—	+	43B
Dorsal vermiculation	×	+	44A
Dorsal spot size	×	+	44B

¹ See Appendix 2 for character descriptions.

TABLE 9

A comparison of OTU 6 for *N. meleagris* with OTUs 3, 7 and 9. × — not significantly different ($P \leq 0.05$; t test); + — OTU 6 significantly greater; — — OTU 6 significantly lower; * — differences delineate OTUs in contour maps.

Character name ¹	OTUs			Contour map Figure no.
	3	7	9	
Bill length	+	+*	+*	34A
Wing length	+	+*	+*	34B
Tarso-metatarsus length	×	+*	+*	35A
Wattle basal width	—	+*	+	35B
Wattle length	+	×	—	36A
Wattle per cent blue	+*	+*	+	36B
Helmet frontal length	+	+*	+*	37A
Helmet rear length	+	—	—*	37B
Helmet central height	+	×	—	38A
Helmet basal length	+	+*	+*	38B
Helmet thickness	+	+*	+*	39A
Cere structure length	+	×	—*	39B
Cere structure thickness	+	×	—*	40A
Collar plumage	+	×	—*	40B
Nape filoplume length	+	+*	+*	41A
Nape filoplume anteroposterior coverage	—	+*	+*	41B
Nape filoplume lateral coverage	—	+	+*	42A
Nape filoplume density	×	+*	+*	42B
Secondary remex outer web vermiculation	—	—	—*	43A
Wing covert barring	—	×	×	43B
Dorsal vermiculation	—	—	—*	44A
Dorsal spot size	+	+	×	44B

¹ See Appendix 2 for character descriptions.

TABLE 10

A comparison of OTU 10 for *N. meleagris* with OTUs 7 and 9. × — not significantly different ($P \leq 0,05$; t test); + — OTU 10 significantly greater; — — OTU 10 significantly lower; * — differences delineate OTUs in contour maps.

Character name ¹	OTUs		Contour map Figure no.
	7	9	
Bill length	—	+	34A
Wing length	—	—	34B
Tarso-metatarsus length	×	+	35A
Wattle basal width	×	×	35B
Wattle length	+	×	36A
Wattle per cent blue	—	—*	36B
Helmet frontal length	+	+	37A
Helmet rear length	+	+	37B
Helmet central height	+	+	38A
Helmet basal length	+	+	38B
Helmet thickness	+	×	39A
Cere structure length	+	—*	39B
Cere structure thickness	+	—*	40A
Collar featheration	+	—*	40B
Nape filoplume length	—*	+	41A
Nape filoplume anteroposterior coverage	—	+	41B
Nape filoplume lateral coverage	—	+	42A
Nape filoplume density	—	+	42B
Secondary remex outer web vermiculation	+	—*	43A
Wing covert barring	×	×	43B
Dorsal vermiculation	+	×	44A
Dorsal spot size	+	—*	44B

¹ See Appendix 2 for character descriptions.

TABLE 11

A comparison of OTU 7 for *N. meleagris* with OTU 9. × — not significantly different ($P \leq 0,05$; t test); + — OTU 7 significantly greater; — — OTU 7 significantly lower; * — differences delineate OTUs in contour maps.

Character name ¹	OTU 9	Contour map Figure no.
Bill length	+	34A
Wing length	+	34B
Tarso-metatarsus length	+	35A
Wattle basal width	×	35B
Wattle length	—*	36A
Wattle per cent blue	×	36B
Helmet frontal length	—*	37A
Helmet rear length	—*	37B
Helmet central height	—*	38A
Helmet basal length	+	38B
Helmet thickness	—*	39A
Cere structure length	—*	39B
Cere structure thickness	—*	40A
Collar featheration	—*	40B
Nape filoplume length	+	41A
Nape filoplume anteroposterior coverage	+	41B
Nape filoplume lateral coverage	+	42A
Nape filoplume density	+	42B
Secondary remex outer web vermiculation	—*	43A
Wing covert barring	×	43B
Dorsal vermiculation	—*	44A
Dorsal spot size	—*	44B

¹ See Appendix 2 for character descriptions.

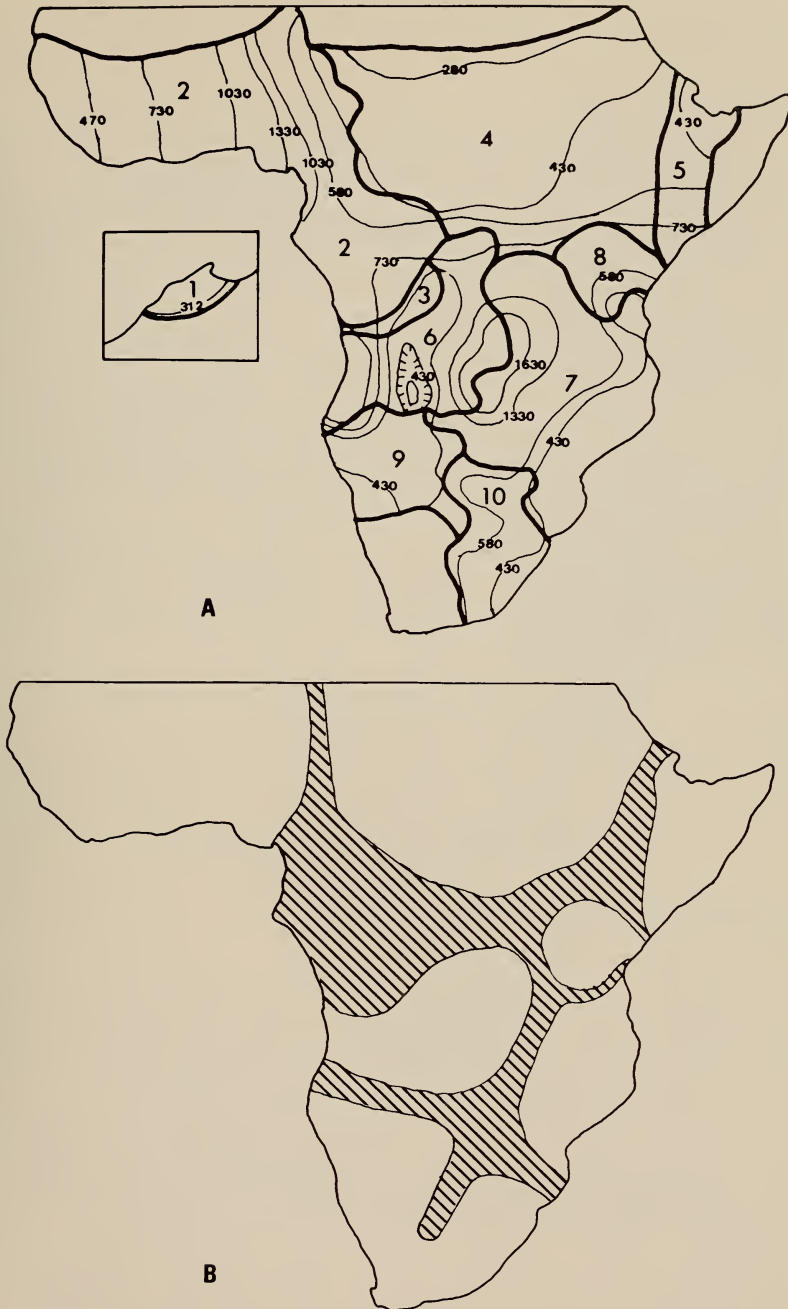


Fig. 45. A. Contour map of total COV in *Numida meleagris* with OTU boundaries indicated by thick lines. B. The approximate distribution of zones of intermediacy between *Numida* OTUs. Larger numbers in A refer to OTU numbers shown in Figure 18B.

The distributions of these subspecies are plotted in Figure 46, and zones of intermediacy are shown in Figure 45B.

TAXONOMIC SUMMARY

In the following classification, verbal descriptions are brief, focusing on more obvious differences and similarities with respect to the qualitative and quantitative characters analysed. For each subspecies, reference is made to its OG or OTU number and the appropriate page(s), tables and figures summarizing its taxonomic relationships and quantitative comparisons with other subspecies. If a synonymized taxon is not discussed, it must be assumed that it did not emerge as an OTU in the cluster analyses. In other words, it was not taxonomically distinct above a level attributable to individual variation in a relatively homogenous population. Subspecies which are mentioned in Table 1, but are not recognized or synonymized, are taken to be intergrades. Herein, an intergrade is a group of taxonomically indeterminable, phenotypically highly variable populations. A population is taken to be taxonomically indeterminable if many of its component individuals show affinities to two or more subspecies (i.e. are classed as intermediates) in discriminant analyses. A population is taken to be highly variable phenotypically if it has a high total COV. See the section on *Taxonomic methodology* for a detailed discussion of OTUs, discriminant analyses and total COV.

Genus *Agelastes*

Agelastes Bonaparte, 1850

Fig. 8(OG1-2)

Agelastes meleagrides Bonaparte, 1850

Figs 1A, 8(OG1)

Agelastes meleagrides Bonaparte, 1850: 145.

Description

Small overall size; no crown, occipital, cere, nape or throat adornments; rudimentary red gape wattles; no feathers on head or neck, skin colour of head and neck red; collar plumage white; body plumage black with faint vermiculations; tarso-metatarsus covered with imbricated scales in rows, and usually with a well-developed spur(s); iris brown; outer margins of secondaries black with faint vermiculations; furcula blade-shaped; abdominal plumage white.

Statistics for quantitative characters (N = 12)

Character	$\bar{X}$	S.D.
Bill length	16,8 mm	1,7
Wing length	205,0 mm	4,8
Tarso-metatarsus length	80,9 mm	3,6
Wattle basal width	6,5 mm	1,2

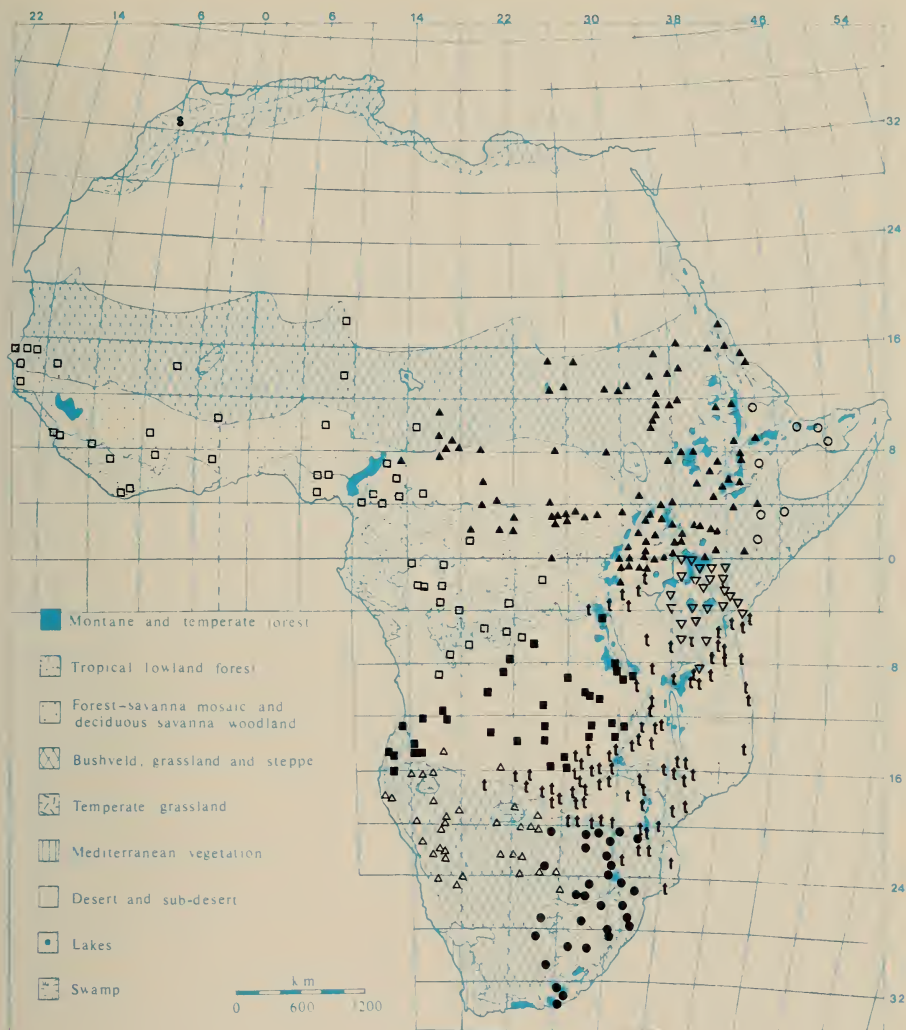


Fig. 46. The distribution of *Numida meleagris*. *N. m. meleagris* (▲). *N. m. sabyi* (s). *N. m. galeata* (□). *N. m. somaliensis* (○). *N. m. marungensis* (■). *N. m. reichenowi* (▽). *N. m. mitrata* (t). *N. m. damarensis* (△). *N. m. coronata* (●).

Character	$\bar{X}$	S.D.
Wattle length	2,7 mm	0,7
Tarsal structure number	0,8	0,6
Tarsal structure length	4,8 mm	3,5
White collar	100,0 %	0,0
Facial filoplumes	0,0	0,0

Distribution

See Figure 10.

Discussion

White collar and facial filoplumes are used as quantitative characters in cluster and discriminant analyses to demonstrate the qualitative distinctness of this taxon from *A. niger*.

Agelastes niger (Cassin, 1857)

Figs 1B, 8(OG2)

Phasidus niger Cassin, 1857: 322.

Description

As *A. meleagrides* except: crown surmounted by a short crest of feathers; nape covered by short, sparsely distributed, black downy feathers; face covered with sparsely distributed filoplumes; collar and abdominal plumage black with faint vermiculations, abdominal plumage white in juveniles.

Statistics for quantitative characters (N = 39)

Character	$\bar{X}$	S.D.
Bill length	16,9 mm	1,5
Wing length	203,0 mm	7,3
Tarso-metatarsus length	79,2 mm	3,4
Wattle basal width	6,5 mm	1,2
Wattle length	2,4 mm	0,6
Tarsal structure number	1,1	0,7
Tarsal structure length	3,4 mm	2,4
White collar	0,0 %	0,0
Facial filoplumes	9,8	0,2

Distribution

See Figure 10.

Discussion

Hall (1961) also advocates the synonymy of *Phasidus* in *Agelastes*, basing her argument largely on analysis of juvenile characters.

Genus *Guttera**Guttera* Wagler, 1832

Fig. 8(OG4-9)

Guttera plumifera plumifera (Cassin, 1857)

Figs 1C, 12A(OTU2), 13(OTU2)

Numida plumifera Cassin, 1857: 321.*Description*

Larger than *Agelastes* spp.; crown surmounted by a crest of long, straight, bristly feathers; small occipital fold of blue-black skin; no nape, throat or cere adornments; well-developed, pointed, blue gape wattles; orbital and throat skin blue-black; collar plumage spotted; body plumage spotted without vermiculations; tarso-metatarsus without spurs, scales pentagonal, not in rows; iris brown; outer margin of secondaries white; furcula blade-shaped; caecum up to 150 mm; abdominal plumage spotted bluish-white without vermiculations.

Statistics for quantitative characters (N = 26)(See p. 65 for statistical comparisons with *G. p. schubotzi*.)

Character	$\bar{X}$	S.D.
Bill length	24,5 mm	1,7
Wing length	225,6 mm	5,9
Tarso-metatarsus length	81,7 mm	3,1
Wattle basal width	10,7 mm	1,2
Wattle length	11,6 mm	2,2
Dorsal spot size	10,7 units	1,0
Crest frontal length	24,6 mm	3,7
Crest rear length	46,9 mm	5,6
Crest central height	31,8 mm	6,7
Crest basal length	30,0 mm	2,6
Anterior crest curliness	1,0	0,0
Posterior crest curliness	1,0	0,0
Dorsal black collar	0,0 %	0,0
Ventral black collar	0,0 %	0,0
Occipital fold	18,3 %	7,5
Ear patch	0,4 mm	0,6
Throat red	0,0 %	0,0
Orbital red	0,0 %	0,0
Dorsal spot number	21,3	3,7
Total spot barbs	5,4	0,6
Total within spot barbs	3,5	0,6

Character	$\bar{X}$	S.D.
Spot barb blueness	0,8	0,6
Chestnut blotch size	0,0 units	0,0
Chestnut blotch extent	0,0 %	0,0

Distribution

See Figure 14.

Guttera plumifera schubotzi Reichenow, 1912

Figs 1D, 12A(OTU1), 13(OTU1)

Guttera plumifera schubotzi Reichenow, 1912: 320.

Description

As *G. p. plumifera*, except that the base of the nape and an area anterior to the ear are covered by patches of orange-yellow skin.

Statistics for quantitative characters (N = 71)

(See p. 65 for statistical comparisons with *G. p. plumifera*)

Character	$\bar{X}$	S.D.
Bill length	22,8 mm	1,4
Wing length	227,2 mm	8,2
Tarso-metatarsus length	80,7 mm	3,4
Wattle basal width	9,6 mm	1,5
Wattle length	8,9 mm	2,4
Dorsal spot size	10,0 units	1,4
Crest frontal length	24,3 mm	5,9
Crest rear length	38,4 mm	4,8
Crest central height	32,4 mm	6,4
Crest basal length	25,9 mm	2,4
Anterior crest curliness	1,0	0,0
Posterior crest curliness	1,0	0,0
Dorsal black collar	0,0 %	0,0
Ventral black collar	0,0 %	0,0
Occipital fold	24,0 %	8,5
Ear patch	15,1 mm	2,8
Throat red	0,0 %	0,0
Orbital red	0,0 %	0,0
Dorsal spot number	21,2	2,9
Total spot barbs	5,7	0,6
Total within-spot barbs	3,7	0,5
Spot barb blueness	1,6	0,6
Chestnut blotch size	0,0 units	0,0
Chestnut blotch extent	0,0 %	0,0

Distribution

See Figure 14.

Discussion

The one intermediate specimen between *G. p. schubotzi* and *G. p. plumifera* is more *schubotzi* in appearance, but the patches of orange on the nape and ear are much reduced in extent.

Guttera pucherani pucherani (Hartlaub, 1860)

Figs 1E, 12A(OTU5), 13(OTU5), Tables 4-5 (OTU5)

Numida pucherani Hartlaub, 1860: 341.

Description

Larger than *G. plumifera*; crown surmounted by a long crest of relatively curly, downy feathers; well-developed occipital fold of blue-black skin; no nape and cere adornments; orbital and throat skin red; throat skin folded; rudimentary, relatively short blue wattles at gape; collar plumage spotted; body plumage spotted without vermiculations; tarso-metatarsus without spurs, scales pentagonal, not in rows; iris red; outer margin of secondaries white; furcula hollow; caecum length up to 150 mm; abdominal plumage spotted bluish-white without vermiculations.

Statistics for quantitative characters (N = 64)

(See Tables 4-5 for statistical comparisons with other subspecies.)

Character	$\bar{X}$	S.D.
Bill length	25,5 mm	1,8
Wing length	261,6 mm	14,8
Tarso-metatarsus length	90,2 mm	6,9
Wattle basal width	9,2 mm	1,5
Wattle length	2,7 mm	0,7
Dorsal spot size	11,3 units	1,3
Crest frontal length	19,4 mm	3,9
Crest rear length	29,5 mm	3,7
Crest central height	26,4 mm	6,6
Crest basal length	34,7 mm	3,2
Anterior crest curliness	1,0	0,2
Posterior crest curliness	2,0	0,2
Dorsal black collar	5,3 %	7,5
Ventral black collar	7,4 %	10,4
Occipital fold	74,6 %	19,5
Ear patch	0,0 mm	0,0
Throat red	98,0 %	12,7
Orbital red	95,4 %	2,4

Character	$\bar{X}$	S.D.
Dorsal spot number	26,0	4,3
Total spot barbs	6,3	1,3
Total within spot barbs	4,3	0,7
Spot barb blueness	1,9	0,9
Chestnut blotch size	0,0 units	0,0
Chestnut blotch extent	0,0 %	0,0

Distribution

See Figure 31.

Discussion

From breeding experiments with captive birds, Ghigi (1936) demonstrated complete interfertility between individuals ascribed to *G. edouardi* and *G. pucherani*. He also found that red throat and orbital skin, characters used to distinguish *G. pucherani*, were invariably absent among F1 hybrids. This suggests that these character states may be recessive. Ghigi (1936) further hypothesized that *Guttera edouardi suahelica* (Neumann 1908: 14) and *G. e. granti* (Elliot 1871: 584), subspecies described from specimens collected in southern Tanzania, are in fact intergrades between *G. p. pucherani* and *G. p. barbata*. The results of this study support that hypothesis, since *pucherani-barbata* intermediates in discriminant analysis (Fig. 13) almost invariably fit descriptions of these taxa, and the distribution attributed to them falls in the high total COV region between the suggested parental subspecies (Fig. 30B).

Guttera pucherani verreauxi (Elliot, 1870)

Figs 1F, 12A(OTU3), 13(OTU3), Table 4(OTU3)

Numida verreauxi Elliot, 1870: 300.

Guttera cristata sethsmithi Neumann, 1908: 13.

Guttera pallasi Stone, 1912: 208.

Guttera edouardi schoutedeni Chapin, 1923: 73.

Guttera edouardi chapini Frade, 1926: 139.

Guttera edouardi kathleenae White, 1943: 19.

Description

As *G. p. pucherani*, except crest longer; less well-developed occipital fold; orbital skin colour blue; collar plumage black with no vermiculations; spotting with stronger blue hue; iris brown.

Statistics for quantitative characters (N = 159)

(See Table 4 for statistical comparisons with other subspecies.)

Character	$\bar{X}$	S.D.
Bill length	23,8 mm	1,6
Wing length	249,2 mm	11,2

Character	$\bar{X}$	S.D.
Tarso-metatarsus length	89,2 mm	4,2
Wattle basal width	9,2 mm	1,2
Wattle length	2,7 mm	0,8
Dorsal spot size	9,5 units	1,5
Crest frontal length	21,1 mm	4,2
Crest rear length	37,4 mm	6,0
Crest central height	26,5 mm	5,8
Crest basal length	31,9 mm	2,6
Anterior crest curliness	1,1	0,3
Posterior crest curliness	2,0	0,2
Dorsal black collar	21,1 %	6,6
Ventral black collar	27,5 %	6,8
Occipital fold	47,1 %	18,4
Ear patch	0,0 mm	0,0
Throat red	91,7 %	13,3
Orbital red	0,0 %	0,0
Dorsal spot number	24,1	3,8
Total spot barbs	6,0	0,7
Total within-spot barbs	3,9	0,7
Spot barb blueness	2,3	0,6
Chestnut blotch size	0,0 units	0,0
Chestnut blotch extent	0,0 %	0,0

Distribution

See Figure 31.

Guttera pucherani sclateri Reichenow, 1898

Figs 1G, 12A(OTU4), 13(OTU4), Table 4(OTU4)

Guttera sclateri Reichenow, 1898b: 115.

Description

As *G. p. verreauxi*, except anterior crest much shorter.

Statistics for quantitative characters (N = 12)

(See Table 4 for statistical comparisons with other subspecies.)

Character	$\bar{X}$	S.D.
Bill length	25,2 mm	2,2
Wing length	245,6 mm	10,4
Tarso-metatarsus length	89,9 mm	4,5
Wattle basal width	10,4 mm	1,2
Wattle length	2,3 mm	0,5
Dorsal spot size	11,5 units	1,5
Crest frontal length	5,8 mm	2,7

Character	$\bar{X}$	S.D.
Crest rear length	40,8 mm	7,2
Crest central height	18,5 mm	4,2
Crest basal length	32,1 mm	4,1
Anterior crest curliness	1,1	0,3
Posterior crest curliness	2,1	0,3
Dorsal black collar	18,0 %	2,7
Ventral black collar	23,5 %	5,1
Occipital fold	62,5 %	17,6
Ear patch	0,0 mm	0,0
Throat red	95,3 %	6,6
Orbital red	0,0 %	0,0
Dorsal spot number	21,3	2,1
Total spot barbs	6,3	0,8
Total within-spot barbs	4,3	0,8
Spot barb blueness	1,8	0,5
Chestnut blotch size	0,0 units	0,0
Chestnut blotch extent	0,0 %	0,0

Distribution

See Figure 31.

Guttera pucherani barbata Ghigi, 1905

Figs 1H, 12A(OTU6), 13(OTU6), Table 5(OTU6)

Guttera barbata Ghigi, 1905: 194.

Description

As *G. p. pucherani*, except crest longer; throat and orbital skin blue; collar plumage black with no vermiculation; body plumage spots occasionally interspersed with chestnut blotches.

Statistics for quantitative characters (N = 28)

(See Table 5 for statistical comparisons with other subspecies.)

Character	$\bar{X}$	S.D.
Bill length	25,3 mm	1,3
Wing length	264,7 mm	11,0
Tarso-metatarsus length	90,2 mm	4,5
Wattle basal width	9,4 mm	1,3
Wattle length	2,8 mm	0,8
Dorsal spot size	10,9 units	1,2
Crest frontal length	23,3 mm	3,7
Crest rear length	32,2 mm	3,9
Crest central height	26,9 mm	8,5
Crest basal length	34,6 mm	2,9

Character	$\bar{X}$	S.D.
Anterior crest curliness	1,1	0,3
Posterior crest curliness	1,9	0,3
Dorsal black collar	21,4 %	4,5
Ventral black collar	26,5 %	5,5
Occipital fold	76,4 %	11,3
Ear patch	0,0 mm	0,0
Throat red	6,9	25,8
Orbital red	0,3	3,9
Dorsal spot number	25,9	4,9
Total spot barbs	5,9	0,7
Total within-spot barbs	4,0	0,5
Spot barb blueness	1,5	0,7
Chestnut blotch size	2,7 units	1,1
Chestnut blotch extent	4,8 %	2,6

Distribution

See Figure 31.

Discussion

Ghigi (1936) mentions *G. p. barbata* specimens with brown irides. This is further evidence of gene flow between the brown-eyed western and red-eyed eastern subspecies of *G. pucherani*.

Guttera pucherani edouardi (Hartlaub, 1867)

Figs 11, 12A(OTU7), 13(OTU7), Tables 4–5(OTU7)

Numida edouardi Hartlaub, 1867: 36.

Guttera lividicollis Ghigi, 1905: 195.

Guttera edouardi symonsi Roberts, 1917: 3.

Description

As *G. p. barbata*, except crest curlier; occipital fold is of whitish skin; no throat fold; black collar plumage extensively covered with chestnut blotching.

Statistics for quantitative characters (N = 34)

Character	$\bar{X}$	S.D.
Bill length	25,6 mm	4,9
Wing length	255,8 mm	7,4
Tarso-metatarsus length	86,9 mm	4,8
Wattle basal width	9,9 mm	1,0
Wattle length	2,5 mm	0,6
Dorsal spot size	9,9 units	1,0
Crest frontal length	22,6 mm	4,7
Crest rear length	38,0 mm	4,1

Character	$\bar{X}$	S.D.
Crest central height	25,9 mm	5,3
Crest basal length	32,8 mm	2,4
Anterior crest curliness	1,5	0,7
Posterior crest curliness	2,1	0,3
Dorsal black collar	27,4 %	4,8
Ventral black collar	32,8 %	4,7
Occipital fold	55,8 %	9,6
Ear patch	0,0 mm	0,0
Throat red	0,0 %	0,0
Orbital red	0,0 %	0,0
Dorsal spot number	23,7	4,2
Total spot barbs	5,2	0,7
Total within-spot barbs	3,5	0,6
Spot barb blueness	0,8	0,5
Chestnut blotch size	10,8 units	3,4
Chestnut blotch extent	54,2 %	19,7

Distribution

See Figure 31.

Genus *Acryllium*

Acryllium Gray, 1840

Fig. 8(OG3)

Acryllium vulturinum (Hardwicke, 1834)

Fig. 1J

Numida vulturina Hardwicke, 1834: 52.

Description

The largest guinea-fowl species; no crown, nape, throat or cere adornments; occiput covered by short, dense, downy chestnut-coloured feathers; rudimentary blue-grey wattles at gape; orbital and throat skin blue-grey; well-developed collar hackle; body plumage spotted with vermiculations; tarso-metatarsus usually with bump(s), scales pentagonal, not in rows; iris red; outer margins of secondaries lavender; furcula blade-shaped; caecum longer than 200 mm; abdominal plumage blue.

Statistics for quantitative characters (N = 43)

Character	$\bar{X}$	S.D.
Bill length	28,5 mm	2,0
Wing length	293,3 mm	10,1
Tarso-metatarsus length	106,0 mm	6,9
Wattle basal width	7,2 mm	1,1

Character	$\bar{X}$	S.D.
Wattle length	2,2 mm	0,6
Tarsal structure number	1,8	1,4
Tarsal structure length	2,6 mm	1,9

Distribution

See Figure 10.

Genus *Numida*

Numida Linne, 1766

Fig. 8(OG10-14)

Numida meleagris meleagris (Linne, 1758)

Figs 1K, 12B(OTU4), 32(OTU4), Table 6(OTU4)

Phasianus meleagris Linne, 1758: 158.

Numida ptilorhyncha var. *major* Hartlaub, 1884: 217.

Numida ptilorhyncha omoensis Neumann, 1904: 407.

Numida ptilorhyncha toruensis Neumann, 1904: 410.

Numida ptilorhyncha macroceras Erlanger, 1904: 97.

Numida ptilorhyncha neumanni Erlanger, 1904: 97.

Numida ptilorhyncha var. *inermis* DuBois, 1915: 18, 27.

Description

Larger than *Guttera* spp.; crown surmounted by a bony helmet; no occipital or throat adornments; well-developed, rounded, blue gape wattles; nape covered by short, downy feathers; orbital and throat skin blue; cere surmounted by a tuft of cartilaginous bristles; collar black, finely barred with white; body plumage spotted with vermiculations; tarso-metatarsus lacks spurs, scales pentagonal, not in rows; iris brown; outer margins of secondaries banded black and white with vermiculations; furcula blade-shaped; caecum less than 150 mm; abdominal plumage spotted with faint vermiculations.

Statistics for quantitative characters (N = 311)

(See Table 6 for statistical comparisons with neighbouring subspecies.)

Character	$\bar{X}$	S.D.
Bill length	25,0 mm	1,7
Wing length	262,2 mm	12,2
Tarso-metatarsus length	84,3 mm	5,2
Wattle basal width	14,1 mm	1,7
Wattle length	13,5 mm	3,0
Wattle per cent blue	97,1 %	12,1
Helmet frontal length	22,6 mm	10,2
Helmet rear length	11,8 mm	7,5
Helmet central height	11,7 mm	8,0

Character	$\bar{X}$	S.D.
Helmet basal length	19,2 mm	3,0
Helmet thickness	6,4 mm	1,7
Cere structure length	6,0 mm	3,6
Cere structure thickness	1,1 mm	0,4
Collar plumage	2,9	0,6
Nape filoplume length	14,9 mm	2,7
Nape filoplume anteroposterior coverage	58,3 %	17,4
Nape filoplume lateral coverage	95,6 %	15,7
Nape filoplume density	2,9	0,3
Secondary remex outer web vermiculation	5,8	0,7
Wing covert barring	1,5	0,7
Dorsal vermiculation	3,0	0,7
Dorsal spot size	18,8 units	5,7

Distribution

See Figure 46.

Discussion

Two taxa, *N. m. strasseni* (Reichenow, 1911: 82) and *N. m. blancoui* (Grote 1936: 158), have been described from the region in which *N. m. galeata* and *N. m. meleagris* meet. Specimens attributed to these taxa are invariably intermediate between *galeata* and *meleagris* in discriminant analysis, and their collection sites fall in the region of high total COV between the parental forms (Fig. 45A). They are treated as intergrades.

Numida meleagris sabyi Hartert, 1919

Figs 1L, 12B(OTU1), 32(OTU1), Table 7(OTU1)

Numida sabyi Hartert, 1919: 69.

Description

As *N. m. meleagris*, except gape wattles red; nape featheration long filoplumes restricted to the mid-dorsal line; no cere adornment.

Statistics for quantitative characters (N = 4)

(See Table 7 for statistical comparisons with neighbouring subspecies.)

Character	$\bar{X}$	S.D.
Bill length	24,0 mm	0,8
Wing length	267,3 mm	10,3
Tarso-metatarsus length	88,3 mm	3,1
Wattle basal width	15,5 mm	1,0
Wattle length	17,8 mm	1,7
Wattle per cent blue	0,0 %	0,0

Character	$\bar{X}$	S.D.
Helmet frontal length	22,5 mm	3,0
Helmet rear length	15,0 mm	6,5
Helmet central height	16,3 mm	2,6
Helmet basal length	20,0 mm	3,4
Helmet thickness	5,3 mm	0,5
Cere structure length	0,0 mm	0,0
Cere structure thickness	0,0 mm	0,0
Collar plumage	2,5	0,6
Nape filoplume length	34,0 mm	7,1
Nape filoplume anteroposterior coverage	100,0 %	0,0
Nape filoplume lateral coverage	85,0 %	17,9
Nape filoplume density	3,0	0,0
Secondary remex outer web vermiculation	3,8	1,5
Wing covert barring	0,0	0,0
Dorsal vermiculation	2,5	0,6
Dorsal spot size	7,2	0,5

Distribution

See Figure 46.

Discussion

Although this taxon is represented by only four specimens, its validity was upheld owing to its isolation and correspondence with criteria set for subspecies.

Numida meleagris galeata Pallas, 1767

Figs 1M, 12B(OTU2), 32(OTU2), Tables 6-7(OTU2)

Numida galeata Pallas, 1767: 13, 15.

Numida marcheii Oustalet, 1882: 1.

Description

As *N. m. sabyi*, except smaller with collar plumage grey to blue-grey.

Statistics for quantitative characters (N = 137)

(See Tables 6-7 for statistical comparisons with neighbouring subspecies.)

Character	$\bar{X}$	S.D.
Bill length	22,3 mm	1,8
Wing length	251,4 mm	14,6
Tarso-metatarsus length	81,8 mm	6,4
Wattle basal width	14,2 mm	1,9
Wattle length	15,5 mm	2,9
Wattle per cent blue	8,3 %	4,3

Character	$\bar{X}$	S.D.
Helmet frontal length	15,5 mm	5,8
Helmet rear length	7,0 mm	2,5
Helmet central height	5,8 mm	2,9
Helmet basal length	18,6 mm	3,3
Helmet thickness	4,9 mm	1,5
Cere structure length	0,3 mm	0,9
Cere structure thickness	0,3 mm	1,6
Collar plumage	0,1	0,3
Nape filoplume length	20,4 mm	4,3
Nape filoplume anteroposterior coverage	90,9 %	16,0
Nape filoplume lateral coverage	70,8 %	33,3
Nape filoplume density	2,8	0,4
Secondary remex outer web vermiculation	4,4	1,3
Wing covert barring	0,6	0,2
Dorsal vermiculation	3,6	0,6
Dorsal spot size	12,2 units	3,8

Distribution

See Figure 46.

Numida meleagris somaliensis Neumann, 1899

Figs 1N, 12B(OTU5), 32(OTU5), Tables 6, 8(OTU5)

Numida somaliensis Neumann, 1899: 25.

Description

As *N. m. meleagris*, except gape wattles blue with red tips; cere tufts much longer and more numerous; and nape featheration long filoplumes restricted to the middorsal line.

Statistics for quantitative characters (N = 44)

(See Tables 6, 8 for statistical comparisons with neighbouring subspecies.)

Character	$\bar{X}$	S.D.
Bill length	25,1 mm	1,4
Wing length	265,5 mm	11,0
Tarso-metatarsus length	84,2 mm	4,2
Wattle basal width	13,6 mm	2,4
Wattle length	14,6 mm	3,3
Wattle per cent blue	87,5 %	14,9
Helmet frontal length	20,0 mm	7,6
Helmet rear length	10,3 mm	6,0
Helmet central height	12,9 mm	12,3

Character	$\bar{X}$	S.D.
Helmet basal length	17,4 mm	3,9
Helmet thickness	6,6 mm	1,3
Cere structure length	13,3 mm	7,6
Cere structure thickness	1,0 mm	0,1
Collar plumage	3,0	0,7
Nape filoplume length	15,8 mm	3,1
Nape filoplume anteroposterior coverage	41,5 %	20,7
Nape filoplume lateral coverage	53,3 %	34,0
Nape filoplume density	2,8	0,5
Secondary remex outer web vermiculation	5,2	2,0
Wing covert barring	0,8	0,6
Dorsal vermiculation	2,4	0,9
Dorsal spot size	23,6 units	6,5

Distribution

See Figure 46.

Numida meleagris marungensis Schalow, 1884

Figs 10, 12B(OTU6), 32(OTU6), Tables 6–7, 9(OTU6)

Numida coronata marungensis Schalow, 1884: 105.

Numida marungensis maxima Neumann, 1898: 21.

Description

The largest subspecies; helmet characteristically thicker and longer basally; long gape wattles, blue with red tips; no cere adornment, and wattles pointed.

Statistics for quantitative characters (N = 97)

(See Tables 6–7, 9 for statistical comparisons with neighbouring subspecies.)

Character	$\bar{X}$	S.D.
Bill length	26,7 mm	1,4
Wing length	283,5 mm	11,1
Tarso-metatarsus length	90,2 mm	4,7
Wattle basal width	11,8 mm	1,5
Wattle length	16,6 mm	3,1
Wattle per cent blue	73,6 %	8,5
Helmet frontal length	47,7 mm	8,5
Helmet rear length	13,4 mm	5,1
Helmet central height	18,7 mm	3,8
Helmet basal length	39,2 mm	3,7
Helmet thickness	12,4 mm	2,6
Cere structure length	0,3 mm	0,7
Cere structure thickness	0,3 mm	0,9

Character	$\bar{X}$	S.D.
Collar plumage	2,9	0,7
Nape filoplume length	26,3 mm	3,3
Nape filoplume anteroposterior coverage	77,3 %	17,5
Nape filoplume lateral coverage	29,6 %	17,5
Nape filoplume density	2,9	0,4
Secondary remex outer web vermiculation	0,9	1,0
Wing covert barring	0,0	0,0
Dorsal vermiculation	1,5	0,8
Dorsal spot size	23,5 units	4,5

Distribution

See Figure 46.

Discussion

N. m. frommi (Kothe 1911: 13) and *N. m. rikwae* (Reichenow 1900: 40) have been described from the region between *N. m. marungensis* and *N. m. mitrata*, and *N. m. callewaerti* (Chapin 1932b: 1) from the region between *N. m. galeata* and *N. m. marungensis*. Specimens attributed to these three forms are invariably intermediate between two subspecies in discriminant analyses, and their collection localities fall within regions of high total COV (Fig. 45A). They are treated as intergrades.

Numida meleagris reichenowi Ogilvie-Grant, 1894

Figs 1P, 12B(OTU8), 32(OTU8), Tables 6, 8(OTU8)

Numida reichenowi Ogilvie-Grant, 1894: 536.

Description

Similar to, and nearly as large as *N. m. marungensis*; except wattles rounded and red, helmet taller and sabre-shaped, and nape featheration less dense.

Statistics for quantitative characters (N = 121)

(See Tables 6, 8 for statistical comparisons with neighbouring subspecies.)

Character	$\bar{X}$	S.D.
Bill length	24,7 mm	1,6
Wing length	282,2 mm	9,1
Tarso-metatarsus length	90,7 mm	11,4
Wattle basal width	11,9 mm	1,4
Wattle length	12,8 mm	2,5
Wattle per cent blue	12,9 %	29,2
Helmet frontal length	44,2 mm	10,9
Helmet rear length	29,5 mm	9,8
Helmet central height	29,5 mm	9,0

Character	$\bar{X}$	S.D.
Helmet basal length	24,9 mm	2,9
Helmet thickness	8,3 mm	1,7
Cere structure length	0,7 mm	1,8
Cere structure thickness	0,4 mm	0,8
Collar plumage	2,9	0,5
Nape filoplume length	20,5 mm	3,6
Nape filoplume anteroposterior coverage	63,8 %	49,2
Nape filoplume lateral coverage	30,0 %	21,3
Nape filoplume density	2,5	0,6
Secondary remex outer web vermiculation	2,3	1,3
Wing covert barring	0,2	0,5
Dorsal vermiculation	2,4	0,7
Dorsal spot size	23,2 units	3,5

Distribution

See Figure 46.

Discussion

N. m. intermedia (Neumann 1898: 21), and *N. m. ansorgei* (Hartert 1899: 331) have been described from the transition area between *N. m. meleagris* and *N. m. reichenowi*. *N. m. uhehensis* (Reichenow 1898a: 88) has been described from the transition area between *N. m. mitrata* and *N. m. reichenowi*. For reasons given in other such instances, these forms are treated as intergrades.

Numida meleagris mitrata Pallas, 1767

Figs 1Q, 12B(OTU7), 32(OTU7), Tables 6, 8–10(OTU7)

Numida mitrata Pallas, 1767: 18.

Description

Smaller than the last two subspecies; phenotype as *N. m. marungensis* except that helmet less well developed.

Statistics for quantitative characters (N = 293)

(See Tables 6, 8–10 for statistical comparisons with neighbouring subspecies.)

Character	$\bar{X}$	S.D.
Bill length	25,7 mm	1,3
Wing length	275,4 mm	8,2
Tarso-metatarsus length	86,1 mm	4,2
Wattle basal width	10,9 mm	1,5
Wattle length	16,8 mm	3,0
Wattle per cent blue	64,6 %	9,3

Character	$\bar{X}$	S.D.
Helmet frontal length	38,3 mm	9,5
Helmet rear length	18,8 mm	5,1
Helmet central height	19,4 mm	7,9
Helmet basal length	23,3 mm	3,8
Helmet thickness	8,3 mm	2,0
Cere structure length	0,2 mm	0,8
Cere structure thickness	0,2 mm	0,7
Collar plumage	3,1	0,6
Nape filoplume length	23,0 mm	3,9
Nape filoplume anteroposterior coverage	59,1 %	19,7
Nape filoplume lateral coverage	23,0 %	8,3
Nape filoplume density	2,5	0,7
Secondary remex outer web vermiculation	1,5	1,3
Wing covert barring	0,0	0,0
Dorsal vermiculation	2,2	0,7
Dorsal spot size	19,4 units	4,5

Distribution

See Figure 46.

Numida meleagris coronata Gurney, 1868

Figs 1R, 12B(OTU10), 32(OTU10), Table 10(OTU10)

Numida coronata Gurney, 1868: 253.

Numida transvaalensis Neumann, 1899: 26.

Numida papillosa limpopoensis Roberts, 1924: 77.

Description

As *N. m. marungensis*, except smaller overall size; decidedly thinner and taller helmet, collar plumage more streaked than barred with white.

Statistics for quantitative characters (N = 136)

(See Table 10 for statistical comparisons with neighbouring subspecies.)

Character	$\bar{X}$	S.D.
Bill length	25,1 mm	1,7
Wing length	270,9 mm	7,0
Tarso-metatarsus length	85,6 mm	5,2
Wattle basal width	11,0 mm	1,5
Wattle length	18,7 mm	3,2
Wattle per cent blue	61,5 %	10,0
Helmet frontal length	54,8 mm	9,6
Helmet rear length	25,1 mm	5,8
Helmet central height	24,7 mm	5,3
Helmet basal length	25,8 mm	2,9

Character	$\bar{X}$	S.D.
Helmet thickness	8,8 mm	2,1
Cere structure length	0,4 mm	0,7
Cere structure thickness	0,3 mm	0,4
Collar plumage	4,2	1,1
Nape filoplume length	18,5 mm	4,6
Nape filoplume anteroposterior coverage	40,0 %	22,8
Nape filoplume lateral coverage	15,3 %	4,9
Nape filoplume density	1,2	0,8
Secondary remex outer web vermiculation	2,5	1,4
Wing covert barring	0,0	0,0
Dorsal vermiculation	2,6	0,6
Dorsal spot size	20,4 units	5,6

Distribution

See Figure 46.

Discussion

Numida meleagris papillosa (Reichenow 1894: 145) has been described from the region south of Lake Ngami, i.e. the transition area between *N. m. damarensis* and *N. m. coronata*. For reasons given in other instances this form is taken to be an intergrade.

Numida meleagris damarensis Roberts, 1917

Figs 1S, 12B(OTU9), 32(OTU9), Tables 9–11(OTU9)

Numida papillosa damarensis Roberts, 1917: 2.

Description

As *N. m. coronata*, except well-developed papilli at cere; collar spotted; helmet less well developed.

Statistics for quantitative characters (N = 102)

(See Tables 9–11 for statistical comparisons with neighbouring subspecies.)

Character	$\bar{X}$	S.D.
Bill length	24,6 mm	1,6
Wing length	273,2 mm	7,6
Tarso-metatarsus length	83,4 mm	3,9
Wattle basal width	11,1 mm	1,3
Wattle length	18,9 mm	2,8
Wattle per cent blue	64,4 %	8,5
Helmet frontal length	45,2 mm	7,5
Helmet rear length	22,9 mm	4,6
Helmet central height	22,3 mm	4,3

Character	$\bar{X}$	S.D.
Helmet basal length	19,7 mm	3,1
Helmet thickness	9,2 mm	1,3
Cere structure length	3,7 mm	1,5
Cere structure thickness	2,9 mm	0,3
Collar plumage	4,9	1,0
Nape filoplume length	12,3 mm	8,5
Nape filoplume anteroposterior coverage	24,7 %	27,2
Nape filoplume lateral coverage	9,7 %	8,0
Nape filoplume density	0,5	0,7
Secondary remex outer web vermiculation	3,8	1,4
Wing covert barring	0,0	0,0
Dorsal vermiculation	2,6	0,5
Dorsal spot size	22,5 units	8,5

Distribution

See Figure 46.

PHYLOGENY

PRIMITIVE AND DERIVED CHARACTER STATES

The following hypothetical primitive-derived sequences are postulated for the characters listed in Appendix 1. The number in parentheses following each character name is its number in Appendix 1.

Crown (1), occipital (2), nape (3), and throat (6) adornments

All francolins and guineafowl-phasianid hybrids have feathered crowns, occiputs and napes. Very few francolins have crests, and then only rudimentary ones. No francolin has a throat fold. Therefore, a naked crown, nape or occiput is taken to be derived relative to the feathered condition. Among guinea-fowl with feathered crowns, a well-developed crest of downy feathers is taken to be derived relative to a short crest of downy feathers, and a well-developed crest of bristly, erect filoplumes derived relative to a well-developed crest of downy feathers. The latter assumption is based on the idea that a modification of a downy, drooping crest to an erect bristly crest allows species or individual recognition in social encounters. Also, among guinea-fowl which have these regions unfeathered, any likely secondary elaboration of the unfeathered condition (e.g. a helmet, long filoplumes, patches of skin of contrasting colour, folds of skin) is taken to be derived, since these structures may be adaptive in a social (individual and species identification) or physio-ecological (thermoregulation, crypsis) context (Brown 1963; Reynolds 1977). Finally, folded throat skin is taken to be derived relative to the unfolded condition.

Orbital (4), throat (5), and gape wattle (8) skin colour

In nearly all francolins, areas of naked skin on the head and throat are red. Therefore, red is taken to be the primitive condition relative to any other colour for the above characters.

Gape adornment (7)

No francolin has a gape wattle, and guineafowl-phasianid hybrids have at most rudimentary wattles. Therefore, well-developed gape wattles are taken to be derived.

Cere adornment (9)

No francolin or guineafowl-phasianid hybrid has an adornment at the cere. Therefore, any cere adornment is taken to be derived.

Collar (10), body (11) and abdominal (18) plumage

The plumage of francolins and guineafowl-phasianid hybrids is usually dark, often streaked, barred or vermiculated with lighter colours. Moreover, none of the above possesses an elaborate collar-hackle. Therefore, among guinea-fowl, white or blue plumage is taken to be derived relative to dark plumage, and spotted plumage derived relative to barred, streaked or vermiculated plumage. Among guinea-fowl with spotted plumage, spotted plumage without peripheral vermiculation is taken to be derived relative to that with vermiculation. Also, regardless of plumage pattern, an elaborate collar hackle is taken to be derived relative to an undifferentiated collar.

Tarso-metatarsal scales (12) and adornment (13)

All francolins have their posterior tarso-metatarsus covered by small imbricated scales in rows. In nearly all francolins, the male at least possesses spurs. Therefore, among guinea-fowl any modification of the spurred condition (e.g. naked tarsi or tarsal bumps), and any scalation pattern other than that described above are taken to be derived conditions.

Iris colour (14)

Nearly all francolins have brown eyes. Therefore, among guinea-fowl, a red iris is taken to be derived.

Outer margins of secondaries (15)

In most francolins the secondaries are brown to grey, sometimes faintly streaked or vermiculated with white. In only a few francolins do the outer margins of these feathers appear to be strikingly different from the general body plumage. Therefore, among guinea-fowl, secondaries that contrast with the general body plumage pattern, i.e. character states 2-4, are taken to be derived.

Furcula (16)

All francolins have blade-shaped furculas. Therefore, a hollow furcula is taken to be derived.

Caecum length (17)

In francolin and guinea-fowl of the genera *Numida* and *Guttera* caecum length is about 16 per cent that of the large and small intestines combined (Beddard 1898). There is no information on caecum length for *Agelastes* spp. In *Acryllium vulturinum*, the length of this organ is more than 23 per cent that of the intestines (Beddard 1898). Therefore, among guinea-fowl a relatively long caecum is taken to be derived.

PHYLETIC ANALYSIS

The most parsimonious guinea-fowl phylogeny based on primitive-derived character sequences is given in Figure 47. In this figure, the four shared derived character states comprising character suite 1 delineate the subfamily Numidinae from francolin-like phasianids. These derived character states, common to all guinea-fowl taxa (Ghigi 1936), and their primitive counterparts (in parentheses) are:

1. large size (small size);
2. third and fourth sacral vertebrae with robust transverse processes (only third vertebra with such a process);
3. second metacarpal lacks a backward process (process present);
4. largely naked head with at least rudimentary wattles (feathered head, and no wattles).

Agelastes sp., with their preponderance of primitive character states, probably more closely resemble the proto-guinea-fowl than does any other member of the subfamily. These two species share only one derived character state, white abdominal plumage. Adult *A. niger* (Fig. 1B) shows primitive character states for all characters investigated except for its naked occiput. The white abdominal plumage linking it to *A. meleagrides* (Fig. 1A) is present only in juvenile birds. It is also possible that the additional derived character states attributable to *Agelastes* due to the naked head and neck of *A. meleagrides* are the result of convergent evolution, and do not suggest any closer affinity to other guinea-fowl genera.

Character suite 2 consists of three shared derived character states (spotted body plumage, non-imbricated, pentagonal scalation of the posterior tarso-metatarsi, unspurred tarso-metatarsi) which link the three remaining genera. Character suite 3 consists of three shared derived character states (unfeathered crown, blue orbital and throat skin) which link *Acryllium* (Fig. 1J) and *Numida* (Fig. 1K-S). Character suite 4 consists of four shared derived character states (folded occipital skin, white outer secondary margins, body plumage spotted without peripheral vermiculation, hollow furcula) which link the two *Guttera* species (Fig. 1C-I), and distinguish them from *Acryllium* and *Numida*. Character suite 5 consists of four derived character states (helmeted crown, naked occiput, well-developed wattles, cere with tufts or papilli) which distinguish *Numida* (Fig. 1K-S) from *Acryllium* (Fig. 1J). Character suite 6 consists of three

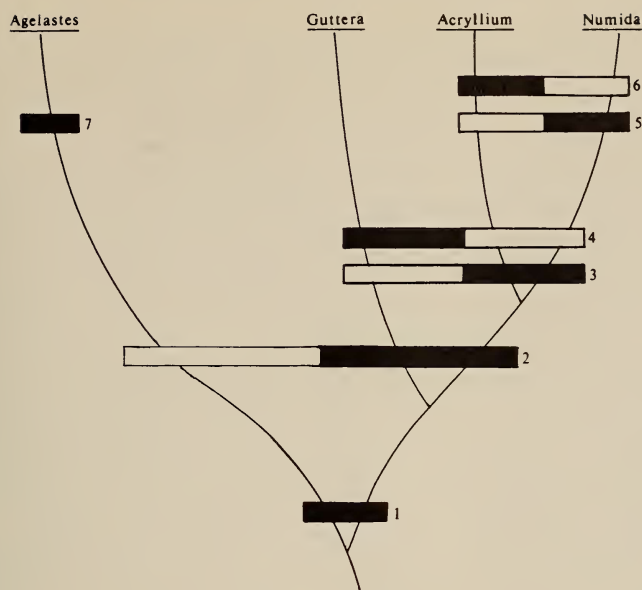


Fig. 47. An hypothetical phylogeny for the Numidinae. Each monophyletic lineage is characterized by a suite of derived character states (■), the primitive counterparts of which (□) are found in members of the co-ordinate sister-group.

derived character states (hackled collar, long caecum, red eye) which distinguish *Acryllium* from *Numida*.

SPECIATION

ORIGIN AND DERIVATION OF THE NUMIDINAE

Several hypotheses have been offered concerning the origin and evolution of the Numidinae. Ghigi (1936) states that the proto-guinea-fowl originated in Africa, and probably was derived from a francolin ancestor. This hypothesis is based on the fact that guinea-fowl are found only in Africa (Arabian and Malagasy populations being probably the result of introductions by man), and phenotypic similarities between the most primitive guinea-fowl (*Agelastes* spp.) and *Francolinus* spp. Cracraft (1973), in support of his hypothesis of a Gondwanaland origin for the Galliformes, suggests a North American origin from New World quails. Olson (1974), suggests a possible Asiatic origin from a pheasant-like bird, based on analysis of a single Eocene fossil femur from Mongolia. This bone is intermediate in shape between femurs of extant pheasants and *Agelastes niger*. However, it is only about 70 per cent the length of an *Agelastes* femur, i.e. well within the size range of many extant francolins (Mackworth-Praed & Grant 1952, 1962, 1970).

There is no compelling evidence favouring any of these three hypotheses. When, and if, sufficient information comes to the fore, it will probably support

elements of all three. Accordingly, the working hypothesis taken herein is: the Numidinae are derived from a francolin-like Asiatic phasianid; but evolution and radiation of extant guinea-fowl has occurred solely in Africa.

EVOLUTION OF GENERA

The first opportunity for colonization of Africa by Asiatic faunal elements arose with the mid-Miocene (*c.* 17–18 m.y.B.P.) union of the African and Asian plates (Axelrod & Raven 1978). At this time, forest was much more extensive in Africa than at present, possibly even exceeding limits depicted in Figure 5. However, the colonization corridor connecting these two continents was covered by relatively arid savanna vegetation in the mid-Miocene, and has almost certainly not had more lush vegetation since then (Axelrod & Raven 1978). Thus, any Asiatic ancestral guinea-fowl was probably a bird which lived in savanna habitat, and, upon its arrival in Africa, encountered vast forest, and much less extensive savanna adaptive zones. Since *Agelastes* spp. possess so few derived character states (see above), it is likely that radiation of proto-*Agelastes* into the forest took place soon after colonization.

With the joining of the two continents, the mild climate that favoured widespread forest vegetation throughout the late Cretaceous and early Tertiary began to deteriorate. Africa became progressively more arid; and savannah and desert–steppe biomes expanded, at the expense of forest, throughout the latter Miocene and Pliocene (Axelrod & Raven 1978). Moreover, this period was characterized by widespread uplifting, rifting and tectonic activity adding considerable topographic diversity to the continent, and partitioning its expanding and contracting biomes (Axelrod & Raven 1978). These conditions would have favoured radiation in and into expanding forest-edge, savanna and desert–steppe biotopes; and it is possible that proto-*Guttera*, *Numida*, and *Acryllium* were the result of such Mio-Pliocene radiations.

EVOLUTION OF SPECIES AND SUBSPECIES

After the uniformly arid Pliocene, the relatively rapid wet–dry climatic fluctuations and continuing rifting and mountain building during the Pleistocene provided additional opportunities for radiation in Africa (Moreau 1966; Hamilton 1974; Livingstone 1975; Axelrod & Raven 1978). Expanding forest and wetlands in relatively moist phases would have divided savanna biome into more or less isolated tracts, and restricted desert to relatively small refugia in Somalia, northern and south-western Africa. If wet-phase forest and wetlands were distributed as in Figure 5, *Acryllium vulturinum* (Fig. 10) and sub-Saharan subspecies attributed to *Numida meleagris* herein (Fig. 46) would have had the opportunity to diverge in isolation, since portions of their present-day ranges are encompassed by isolated tracts of savanna and desert–steppe refugia. Also, expanding forest may have favoured a second radiation into relatively widespread lowland forest, culminating in *Guttera plumifera*.

During arid phases, forest-living guinea-fowl, and Moroccan *N. meleagris*,

would have been restricted to island-like refugia. If vegetation were distributed as in Figure 6, *N. m. sabyi* (Fig. 46), *Agelastes meleagrides* (Fig. 10), *A. niger* (Fig. 10), *Guttera plumifera plumifera* and *G. p. schubotzi* (Fig. 14) and, to a lesser extent, forest-edge taxa (subspecies attributed to *G. pucherani*) had the opportunity to diverge in allopatry, since portions of their present-day ranges would have had access to refuges of suitable biotope. Thus, we need look no further than the Pleistocene for biogeographic events which could have allowed allopatric evolution of extant guinea-fowl species and subspecies.

BIOGEOGRAPHY

RESULTS

A map of hypothetical African avifaunal zones drawn from evolutionary patterns found in guinea-fowl is given as Figure 48. Zonal boundary lines in this map agree remarkably well with those in Chapin's (1932a) faunal map (Fig. 49) based on distribution patterns of 'many species and races of birds', and with species and subspecies boundaries in distribution maps of selected francolin species and subspecies (Figs 50–51). In the hypothetical avifaunal map, subregion boundaries are those of the relatively phenotypically homogeneous (i.e. no subspecies) genera, *Agelastes* and *Acryllium* (Fig. 10). Provincial boundaries coincide closely with those of species, and district boundaries with those of subspecies (Figs 14, 31 and 46). Chapin neither lists the taxa whose ranges form the basis of his map, nor specifies criteria used in distinguishing subregions, provinces and districts. The hypothetical map differs markedly from Chapin's in that it:

1. restricts the forest subregion (commonly labelled ① in Figs 48–49) to an area somewhat larger than Chapin's province no. 1;
2. divides his province no. 4 into eastern and western, rather than northern and southern districts;
3. divides his district 1B into two districts (1A and 1B in Fig. 48).
4. reapportions territory within the commonly labelled province no. 6;
5. divides his district no. 6E into two provinces (7 and 8 in Fig. 48);
6. does not recognize montane provinces.

The only differences between the hypothetical map and the francolin distribution maps are relatively minor shifts in boundary lines, and a still finer subdivision of districts by francolins. Also, district boundaries, which separate guinea-fowl subspecies, often delimit francolin species.

DISCUSSION

It is impossible to resolve differences between the two avifaunal maps in zonal boundaries and hierarchical assessments, since Chapin does not specify the data base and methodology underlying his map. His decision to unite the continuous block of lowland forest with the surrounding forest-savanna mosaic to form subregion ① (Fig. 49) is probably due to the abundance, in



Fig. 48. Hypothetical African avifaunal zones based on evolutionary patterns found in guinea-fowl.

the latter, of relict patches of lowland forest and gallery forests, which provide suitable habitats for forest birds. Indeed, when distributional data are lacking or equivocal, Chapin (1932*a*) and other zoogeographers (e.g. Davis 1962; Moreau 1966) seem to have relied on the distribution of vegetation as a predictor of bird distributions. The division of Chapin's province no. 4 and district 1B into east-west districts in the hypothetical map is due to effects (on guinea-fowl evolution) of probable past forest-wetland and savanna barriers that bisected these zones during the Pleistocene (see Figs 5-6). The reapportionment of territory to districts in the commonly labelled province no. 6 may reflect a lack of clear-cut avian distributional patterns within that province, a possibility already suggested by Benson & Irwin (1966). The necessity of partitioning Chapin's district no. 6E was anticipated by that author (Chapin 1932*a*: 89), and has been done by other authors (Moreau 1952; Davis 1962). The lack of montane avifaunal zones in the hypothetical map is certainly due to the sub-montane altitudinal limitation of guinea-fowl.



Fig. 49. African avifaunal zones based on analysis of bird species and subspecies distributions (after Chapin 1932a).

CONCLUSIONS

The results of comparisons of the hypothetical avifaunal map with Chapin's map and francolin distribution maps suggest three tentative conclusions, which can serve as hypotheses in future evolutionary and biogeographic studies.

1. Distribution patterns found in guinea-fowl can be used as models for broad patterns exhibited by African bird species and subspecies other than those dependent on montane habitats.

2. At least some francolin species and subspecies have evolved as a result of factors that have been important in the evolution of guinea-fowl.

3. Physical and ecological barriers which have allowed only subspeciation in guinea-fowl have been sufficient to bring about speciation in francolins.

The first hypothesis is being tested by a cluster analysis (Hagemier & Stults 1964; Sneath & Sokal 1973) of 119 equally sized areas of Africa according to 1 099 passerine species and well-marked subspecies in Hall & Moreau (1970) (Crowe in prep.). The preliminary results of this study, summarized in Figure 52, are consistent with that hypothesis. The second and third hypotheses can be tested, if patterns of character variation in francolin taxa are analysed using



Fig. 50. Distributions of selected non-forest francolin species and subspecies (after Hall 1963 and Mackworth-Praed & Grant 1952). A. *Francolinus bicalcaratus ayesha*. B. *F. clapper-toni*. C. *F. icterorhynchus*. D. *F. leucoscepus*. E. *F. afer cranchii*, *intercedens* and *harterti*. F. *F. hildebrandti*. G. *F. hartlaubi*. H. *F. adspersus*. I. *F. natalensis*. J. *F. capensis*.

methodology outlined herein, and the results are compared to those for guinea-fowl.

SYNTHESIS

Taxonomy, phylogeny, speciation and biogeography are intimately related aspects of guinea-fowl evolution. Their necessary separation under different headings in the present study has been somewhat detrimental to the understanding of each. Accordingly, this section attempts to synthesize the author's conception of evolution in guinea-fowl (summarized in Fig. 53).

Guinea-fowl are characteristically African birds. Although the likely ancestral guinea-fowl was an Asiatic francolin-like phasianid which could live in arid savanna habitat, the evolution that has led to extant guinea-fowl taxa occurred solely in Africa. Moreover, biogeographic patterns derived from



Fig. 51. Distributions of selected forest-living francolin species and subspecies (after Hall 1963).

guinea-fowl species and subspecies boundaries closely parallel broad patterns found in African birds as a whole. The Asiatic ancestral guinea-fowl probably traversed the arid-savanna corridor linking Asia and Africa soon after the mid-Miocene union of the two continents. This savanna-living bird encountered an African continent dominated by forest, possibly unoccupied by potential competitors. Such conditions favoured radiation into the forest, and it is likely that *Agelastes*, the most primitive (i.e. most francolin-like) guinea-fowl genus is a result of an early radiation into forest.

Relatively soon (on a geological time scale) after this successful invasion of forest, the climate of Africa became more arid. Throughout the latter Miocene and Pliocene savanna and desert biomes expanded at the expense of forest. Such a situation favoured radiation in non-forest biomes, and into the expanding forest-edge biotope, and it is possible that proto-*Numida*, *Acryllium* and

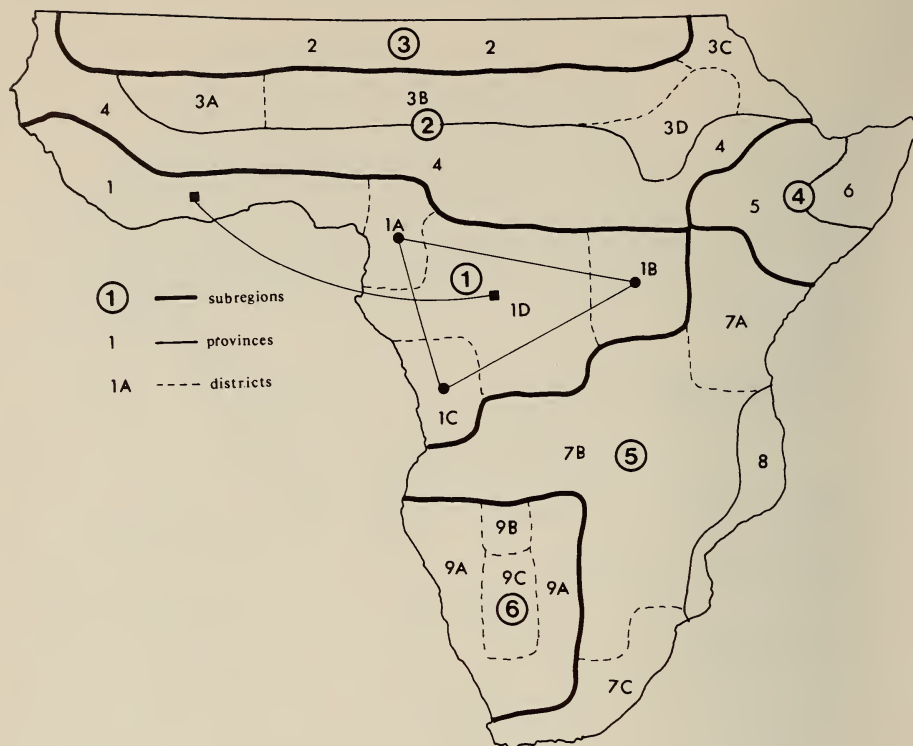


Fig. 52. Hypothetical African avifaunal zones based on a cluster analysis of 119 equally sized blocks of Africa according to 1 099 species and subspecies in Hall & Moreau (1970).

Guttera were the result of such radiations. The relatively uniformly arid conditions of the Pliocene subjected these four lineages to strongly divergent selective pressures, and it is probable that the genera recognized herein were already well defined at the beginning of the Pleistocene.

The arid climate of the Pliocene was replaced by a fluctuating wet-dry climate in the Pleistocene. These climatic fluctuations had profound effects on the distribution of African biomes. During moist phases, the forest biome expanded considerably beyond its present extent, partitioning non-forested biomes into more or less isolated tracts. Desert biome was confined to relatively small areas, and savanna biome bridged the western Sahara, allowing dispersal of *N. meleagris* into north Africa. Sub-saharan subspecies of *N. meleagris* are the result of divergence in these wet-phase isolated tracts. Also, expanded forest during mesic phases could have allowed a second radiation into lowland forest, culminating in *Guttera plumifera*. During arid phases, the forest contracted into island-like refugia, and *N. m. sabyi* was isolated, and presumably diverged from sub-Saharan populations. The species *Agelastes meleagrides* and *A. niger*,

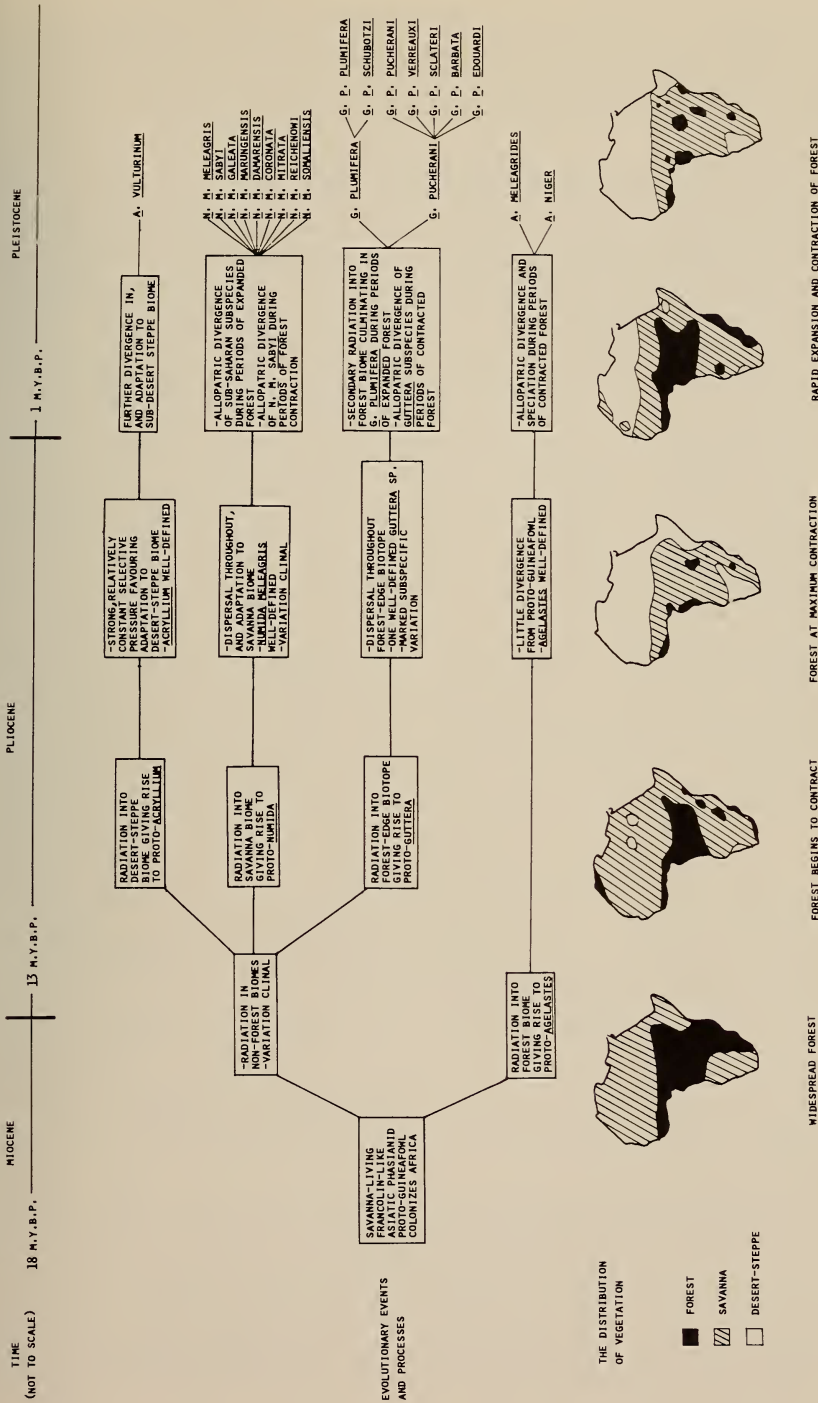


Fig. 53. An hypothetical evolutionary history of guinea-fowl.

and subspecies in the genus *Guttera*, are also a result of divergence in these refugia. The fact that *Guttera* subspecies are much more well marked than are those of *N. meleagris* suggests that isolation in forest refugia has been more effective than in tracts of savanna partitioned during wet phases.

ACKNOWLEDGEMENTS

I am grateful to Mr P. Clancey of the Durban Museum and Art Gallery, Dr F. Gill of the Philadelphia Academy of Natural Sciences, Mr M. Irwin of the National Museum of Rhodesia (Bulawayo), Dr A. Kemp of the Transvaal Museum, Dr M. Louette of the Musée Royal de l'Afrique Centrale, Dr R. Paynter of the Museum of Comparative Zoology, Dr L. Short of the American Museum of Natural History, Dr D. Snow of the British Museum (Natural History), and Major M. Traylor of the Field Museum of Natural History for allowing me access to the guinea-fowl in their institutions' collections. Mrs J. Adams painted the guinea-fowl shown in Figure 1. Mr S. Piper helped with contour maps. Dr L. Throckmorton provided initial encouragement to begin this analysis. Prof. W. R. Siegfried provided the necessary stimulus to finish the analysis. Mr R. Brooke commented critically on several drafts of the paper. My wife, Anna, helped in all phases of the study, particularly with illustrations and data processing. The De Beers and University of Cape Town Computer Centres gave valuable advice on data processing and computer time. Generous grants from De Beers Consolidated Mines Ltd and the University of Cape Town were essential to the project. The inclusion of Figure 1 was made possible by a grant from the University of Cape Town Editorial Board. I should like to thank the South African Museum for publishing this paper.

REFERENCES

- ARCHER, G. A. & GODMAN, E. 1937. *The birds of Somaliland and the Gulf of Aden* 2 London: Gurney & Jackson.
- AXELROD, D. I. & RAVEN, P. H. 1978. Late Cretaceous and Tertiary vegetation history of Africa. In: WERGER, M. J. A., ed. *Biogeography and Ecology of Southern Africa. Monographiae biol.* 31. The Hague: Junk.
- BANNERMAN, D. A. 1930. *Birds of tropical west Africa* 1 London: Crown Agents.
- BEDDARD, F. E. 1898. *The structure and classification of birds*. London: Longmans, Green & Co.
- BENSON, C. W. & IRWIN, M. P. S. 1966. The brachystegia avifauna. *Ostrich*, Suppl. 6: 297-321.
- BOETTICHER, H. V. 1954. *Die Perlhühner*. Wittenberg-Lutherstadt: Ziemsen.
- BONAPARTE, C. 1850. A new species of guinea fowl from West Africa. *Proc. zool. Soc. Lond.* 145.
- BOURKE, D. 1967. The Kazabo. *Niger. Fld* 32: 17-21.
- BROWN, J. L. 1963. Ecogeographic variation and introgression in avian visual signal: the crest of the Steller's Jay, *Cyanocitta stelleri*. *Evolution* 17: 23-39.
- BUTZER, K. W. 1967. Hypothetical rainfall and vegetation zones. In: CLARK, J. DESMOND, ed. *Atlas of African Prehistory*. London: University of Chicago Press.
- CALCOMP. 1971. *GPCP: a general purpose contouring program*. Anaheim: CALCOMP Computer Products Inc.
- CARCASSON, R. H. 1964. A preliminary survey of the zoogeography of African butterflies. *E. Afr. wildl. J.* 2: 122-157.

- CASSIN, J. 1857. Birds collected in West Africa by P. B. du Chaillu. *Proc. Acad. nat. Sci. Philad.* **8**: 322.
- CHAPIN, J. P. 1923. The crested guineafowl of the southern Congo basin. *Revue zool. afr.* **11**: 71-77.
- CHAPIN, J. P. 1932a. The birds of the Belgian Congo. Part I. *Bull. Am. Mus. nat. Hist.* **65**: 1-756.
- CHAPIN, J. P. 1932b. Fourteen new birds from Tropical Africa. *Am. Mus. Novit.* **570**: 1-18.
- COOKE, H. B. S. 1962. The environment in Southern Africa during the Pleistocene. *Ann. Cape Prov. Mus.* **2**: 11-15.
- CRACRAFT, J. 1972. The relationships of the higher taxa of birds: Problems in phylogenetic reasoning. *Condor*. **74**: 379-392.
- CRACRAFT, J. 1973. Continental drift, paleoclimatology and the evolution of birds. *J. Zool. Lond.* **169**: 455-545.
- CROWE, T. M. & SNOW, D. W. 1978. Numididae. In: SNOW, D., ed. *An atlas of speciation in African non-passerine birds*. London: British Museum (Natural History).
- DAVIS, D. H. S. 1962. Distribution patterns of Southern African Muridae, with notes on some of their fossil antecedents. *Ann. Cape Prov. Mus.* **2**: 56-76.
- DIXON, W. J. ed. 1975. *Biomedical computer programs*. University of California Publications In Automatic Computation, No. 5. Berkeley: University of California Press.
- DUBOIS, F. 1915. Remarques sur l'ornithologie de l'état indépendant du Congo suivies d'une liste des espèces jusqu'à cet état. *Annls Mus. Congo., Zool.*, **1**: 18, 27.
- EHRLICH, P. & RAVEN, P. 1969. Differentiation of populations. *Science* **165**: 1228-1232.
- ELGOOD, J. H., FRY, C. H. & DOWSETT, R. J. 1973. African migrants in Nigeria. *Ibis* **115**: 1-45.
- ELLIOT, D. 1870. A description of a new species of crested guinea fowl. *Ibis*: 300-301.
- ELLIOT, D. 1871. Description of a supposed new species of guinea-fowl. *Proc. zool. Soc. Lond.*: 584.
- ERLANGER, C. 1904. Neue Afrikanische arten. *Orn. Mber.* **12**: 97-98.
- FORD, J. 1974. Concepts of subspecies and hybrid zones, and their application in Australian ornithology. *Emu* **74**: 113-123.
- FRADE, F. 1924. Notes d'ornithologie Africaine. *Bull. Soc. port. Sci. nat. Lisbonne* **9**: 136.
- GHIGI, A. 1905. Revisione del genera *Guttera* Wagler. *Mem. R. Accad. Sci. Inst. Bologna* **2**: 189-198.
- GHIGI, A. 1936. *Galline di Faraone e Tacchini*. Milano: V. Hoepli.
- GOULD, S. J. & JOHNSTON, R. F. 1972. Geographic variation. *A. Rev. Ecol. Syst.* **3**: 457-498.
- GRAY, G. R. 1840. *Generic list for birds*: **61**. London.
- GROTE, H. 1936. Das perlhuhn von Noroostkamerun. *Orn. Mber.* **44**: 156-158.
- GURNEY, J. 1868. Notes on Mr. Layard's 'Birds of South Africa'. *Ibis*: 253-271.
- HAGEMIER, E. M. & STULTS, C. D. 1964. A numerical analysis of the distributional patterns of North American mammals. *Syst. Zool.* **13**: 125-155.
- HALL, B. P. 1961. The relationship of the guineafowls *Agelastes meleagrides* Bonaparte and *Phasidus niger* Cassin. *Bull. Br. Orn. Club* **81**: 132.
- HALL, B. P. 1963. The Francolins, A study in speciation. *Bull. Br. Mus. nat. Hist.* **10**: 105-204.
- HALL, B. P. & MOREAU, R. E. 1970. *An atlas of speciation in African passerine birds*. London: British Museum (Natural History).
- HAMILTON, I. 1974. The significance of patterns of distribution shown by forest plants and animals in tropical Africa for the reconstruction of upper Pleistocene palaeoenvironments: a review *Palaeoecology* **9**: 63-97.
- HARDWICKE, T. 1834. Description of a new species of the genus *Numida*. *Proc. zool. Soc. Lond.*: 52.
- HARTERT, E. 1899. In: ANSORGE, W. *Under the African Sun*. New York: Longmans, Green.
- HARTERT, E. 1919. *Numida Sabyi*, a new species of helmeted guinea-fowl. *Bull. Br. Orn. Club* **39**: 69.
- HARTLAUB, G. 1867. Veber eine neue *Numida*. *J. Orn., Lpz.* **15**: 36-37.
- HARTLAUB, G. 1860. Drie neue afrikansche Vögel der Pariser Sammlung. *J. Orn., Lpz.* **8**: 340-341.
- HARTLAUB, G. 1884. Ornithologie der östlich-äquatorialen Gebiete Africas. *Abh. naturw. Ver Bremen* **8**: 183-222.
- HOWELL, F. C. & BOURLIÈRE, F. eds. 1963. *African ecology and human evolution*. Chicago: Aldine.

- JACKSON, F. J. 1938. *The birds of Kenya Colony and the Uganda Protectorate* 1: London: Gurney & Jackson.
- KOTHE, K. 1911. *Numida frommi*; n. sp. *Orn. Mber.* 19: 13–14.
- LINNE, C. 1758. *Systema Naturae*. 10th ed. Stockholm.
- LINNE, C. 1766. *Systema Naturae*. 12th ed. Stockholm.
- LIVINGSTONE, D. A. 1975. Late Quaternary climatic change in Africa. *A. Rev. Ecol. Syst.* 6: 249–280.
- MACKWORTH-PRAED, C. W. & GRANT, C. H. B. 1952. *Birds of eastern and north-eastern Africa*. London: Longmans, Green.
- MACKWORTH-PRAED, C. W. & GRANT, C. H. B. 1962. *Birds of the southern third of Africa*. London: Longmans, Green.
- MACKWORTH-PRAED, C. W. & GRANT, C. H. B. 1970. *Birds of central and western Africa*. London: Longmans, Green.
- MARX, H. & RABB, G. B. 1970. Character analysis: an empirical approach applied to advanced snakes, *J. zool. Lond.* 161: 525–548.
- MAYR, E., LINSLEY, E. G. & USINGER, R. L. 1953. *Methods and principles of systematic zoology*. New York: McGraw-Hill Co.
- MOREAU, R. E. 1952. Africa since the Mesozoic: with particular reference to certain biological problems. *Proc. zool. Soc. Lond.* 121: 869–913.
- MOREAU, R. E. 1957. Variation in Western Zosteropidae (Aves). *Bull. Br. Mus. nat. Hist.* 7: 309–433.
- MOREAU, R. E. 1963. The distribution of tropical African birds as an indicator of post climatic changes. In: HOWELL, F. C. & BOURLIÈRE, F. eds. *Africa Ecology and Human Evolution, Viking Fund Publications in Anthropology* 36: 28–42. Chicago: Aldine.
- MOREAU, R. E. 1966. The birds faunas of Africa and its islands. New York: Academic Press.
- NEUMANN, O. 1898. Die Helmpferlhüner. *Orn. Mber.* 6: 17–22.
- NEUMANN, O. 1899. Neue und wenig bekannte afrikanische Vögel. *Orn. Mber.* 7: 23–26.
- NEUMANN, O. 1904. Vögel von Schoa und süd Aethiopien. *J. Orn., Lpz.* 53: 410.
- NEUMANN, O. 1908. New subspecies of *Guttera cristata*. *Bull. Br. Orn. Club* 23: 13–14.
- OGILVIE-GRANT, W. 1894. On a new species of guineafowl. *Ibis*: 535–538.
- OLSON, S. L. 1974. *Telecrex* restudied: a small Eocene guineafowl. *Wilson Bull.* 86: 246–250.
- OUSTALET, E. 1882. Description d'une nouvelle espece de pintade du Gabon. *Annls Sci. nat. Zool.* 13: 1.
- PALLAS, P. 1767. *Spicilegium Zoologicum* 1: 18. Berolina: Gottl. August Lange.
- PETERS, J. L. 1934. *Check-list of the birds of the world* 2. Cambridge: Harvard University Press.
- PRIEST, C. D. 1933. *The birds of Southern Rhodesia* 1: London: William Clowes & Sons, Ltd.
- REICHENOW, A. 1894. Das Helmpferhuhn von Damaraland. *Orn. Mber.* 2: 145.
- REICHENOW, A. 1898a. Nachrichten. *Orn. Mber.* 6: 88.
- REICHENOW, A. 1898b. *Guttera sclateri* Rchw n. sp. *Orn. Mber.* 6: 115.
- REICHENOW, A. 1900. Neue Forschungen in Deutsch Ostafrika. *Orn. Mber.* 8: 38–40.
- REICHENOW, A. 1911. Neue arten aus Afrika Neuguinea. *Orn. Mber.* 19: 82–83.
- REICHENOW, A. 1912. Neue arten ans dem Velle-Gebied in Mittel-Afrika. *J. Orn., Lpz.* 60: 320–321.
- REYNOLDS, J. F. 1977. Thermo-regulatory problems of birds nesting in East Africa: a review. *Scopus* 1: 57–68.
- ROBERTS, A. 1917. Descriptions of a new species and genus of flycatchers from East Africa and two new subspecies of guinea-fowls from South Africa. *Ann. Transv. Mus.* 6: 1–3.
- ROBERTS, A. 1924. Classification of South African birds. *Ann. Transv. Mus.*, 10: 77–86.
- ROBERTS, T. R. 1975. Geographical distribution of African freshwater fishes. *J. Linn. Soc., Zool.* 57: 249–320.
- SCHALOW, H. 1884. *Numida coronata marungensis* subsp. nov. *Z. Orn. prakt. Geflügelz.* 105.
- SELANDER, R. K. 1971. Systematics and speciation in birds. In: FARNER, D. S. & KING, J. R., eds. *Avian Biology* 1: 57–147.
- SIBLEY, C. G. & AHLQUIST, J. E. 1972. A comparative study of the egg white proteins of non-passerine birds. *Bull. Peabody Mus. nat. Hist.* 39.
- SNEATH, P. H. A. & SOKAL, R. R. 1973. *Numerical Taxonomy*. San Francisco: W. H. Freeman & Co.
- SOKAL, R. R. & ROHLF, F. J. 1969. *Biometry: the principles and practice of statistics in biological research*. San Francisco: W. H. Freeman & Co.

- STONE, W. 1912. Vroeg's catalogue. *Auk*. **29**: 205–208.
- UDVARDY, M. D. F. 1969. *Dynamic zoogeography with special reference to land animals*. New York: Van Nostrand Reinhold Co.
- VUILLEUMIER, B. S. 1971. Pleistocene changes in the fauna and flora of South America. *Science* **173**: 771–780.
- VUILLEUMIER, F. 1975. Zoogeography. In: FARNER, D. S. & KING, J. R. eds. *Avian Biology* **5**: 421–496. New York: Academic Press.
- WAGLER, J. 1832. *Isis*. London: Willoughby Society.
- WETMORE, A. 1960. A classification for the birds of the world. *Smithson. misc. Collns* **139**.
- WHITE, C. 1943. Three new races from Northern Rhodesia. *Bull. Br. Orn. Club* **64**: 19–22.
- WHITE, C. M. N. 1965. *A revised check-list of African non-passerine birds*. Lusaka: The Government Press.
- WILSON, E. O., BROWN, W. L., JR. 1953. The subspecies concept and its taxonomic application. *Syst. Zool.* **2**: 97–111.

APPENDIX 1

Qualitative characters and character states analysed in this study.

No.	Character name	States
1	Crown adornment . . .	1 — short crest of feathers 2 — long crest of feathers 3 — none, only naked skin 4 — bony helmet
2	Occipital adornment . . .	1 — short, dense, chestnut-coloured downy feathers 2 — long filoplumes confined to a mid-dorsal line 3 — fold of blue to black skin 4 — fold of whitish skin 5 — none, only naked skin
3	Nape adornment . . .	1 — short downy feathers 2 — long filoplumes confined to a mid-dorsal line 3 — patch of orange-yellow skin at base, similar patch anterior to ear 4 — none, only naked skin
4	Orbital skin colour . . .	1 — pink to red 2 — light blue to black
5	Throat skin colour . . .	1 — pink to red 2 — blue to black
6	Throat adornment . . .	1 — no fold of skin 2 — fold of skin
7	Gape adornment . . .	1 — rudimentary wattles 2 — well-developed and pointed wattles 3 — well-developed and rounded wattles
8	Gape wattle colour . . .	1 — pink to red 2 — blue to blue-grey 3 — blue with red tips
9	Cere adornment . . .	1 — none 2 — cartilaginous tufts or papilli
10	Collar plumage . . .	1 — black with faint vermiculations 2 — black with no vermiculations 3 — black, finely barred with white 4 — grey to blue-grey 5 — spotted 6 — well-developed hackle 7 — white
11	Body plumage . . .	1 — black with vermiculations 2 — spotted with vermiculations 3 — spotted without vermiculations 4 — as 3, with chestnut blotching between spots

No.	Character name	States
12	Tarso-metatarsal scales	1 — imbricated and in a row 2 — pentagonal, not in rows
13	Tarso-metatarsal adornment	1 — spurs or bumps 2 — none
14	Iris colour	1 — brown 2 — red
15	Outer margins of secondaries	1 — brown to black with faint vermiculation 2 — white 3 — lavender 4 — alternating bands of black and white with varying degrees of black and white vermiculations
16	Furcula	1 — blade-shaped 2 — hollow, cup-shaped; found in guineafowl with long crests (Chapin 1932a)
17	Caecum length	1 — up to 150 mm 2 — greater than 200 mm; in all specimens conforming to the description of <i>Acryllium vulturinum</i> (Beddard 1898)
18	Abdomen plumage	1 — white 2 — blue 3 — white spots with faint vermiculations 4 — bluish-white spots without vermiculations

APPENDIX 2

Quantitative characters analysed in this study. See Figures 1–4 for a pictorial representation of many of the characters.

No.	Name	Units	Description
1	Bill length	mm	the chord measured from the base of the cere to the tip of the maxilla
2	Wing length	mm	the chord of the unflattened folded wing from the farthest anterior tip of the wrist joint to the tip of the longest primary
3	Tarso-metatarsus length	mm	the diagonal chord from the posterior point of articulation of the tarsometatarsus with the tibia to the most distal undivided tarsal scute on the dorsal surface of the middle toe
4	Wattle basal width	mm	the chord from the most anterior to posterior points of juncture of the wattle with the cheek
5	Wattle length	mm	the chord from the juncture line of the wattle to the most distal point along the wattle margin
6	Wattle per cent blue	%	a subjective estimate of the surface area of the wattle covered by blue pigment. It is possible to assess the amount of this colour in preserved material since, although natural colour is lost soon after death, the demarcation between red and blue can be determined because red areas revert to a yellow or translucent amber state, and blue areas to an opaque blue-grey
7	Helmet frontal length	mm	the curvilinear distance, as measured with a flexible tape, along the anterior margin of the bony helmet from the point of juncture with the skull to the apex